ANIMAL BEHAVIOUR

Formerly The British Journal of Animal Behaviour

Editor
ALASTAIR N. WORDEN (Huntingdon)

Associate Editors
L. WEISKRANTZ (Cambridge) *and* D. E. DAVIS (University Park, Pa.)

with the assistance of

L. R. ARONSON (New York)
J. D. CARTHY (London)
N. E. COLLIAS (Los Angeles)
J. T. EAYRS (Birmingham)
A. E. EMERSON (Chicago)
J. T. EMLEN (Madison)
P. E. FIELDS (Seattle, Washington)
G. C. GRINDLEY (Cambridge)
E. B. HALE (University Park, Pa.)
JOHN HAMMOND, F.R.S. (Cambridge)
R. A. HINDE (Cambridge)
JULIAN HUXLEY, F.R.S. (London)
D. S. LEHRMAN (Newark, N.J.)
L. HARRISON MATTHEWS, F.R.S. (London)
C. F. A. PANTIN, F.R.S. (Cambridge)
C. R. RIBBANDS (Cambridge)
A. J. RIOPELLE (Orange Park, Florida)
K. D. ROEDER (Medford, Mass.)
J. P. SCOTT (Bar Harbor)
HARRY V. THOMPSON (London)
W. H. THORPE, F.R.S. (Cambridge)
N. TINBERGEN (Oxford)
W. S. VERPLANCK (New York)
D. M. VOWLES (Oxford)
H. E. WINN (Maryland)
S. ZUCKERMAN, F.R.S. (Birmingham)

VOLUME IX 1961

LONDON
BAILLIÈRE, TINDALL AND COX LTD
7 AND 8 HENRIETTA STREET
W.C.2

CONTENTS OF VOLUME IX

ORIGINAL CONTRIBUTIONS

ABERCROMBIE, BARBARA & JAMES, H. The Stability of the Domestic Chick's Response to Visual Flicker 205

ALABASTER, J. S. & ROBERTSON, K. G. The Effect of Diurnal Changes in Temperature, Dissolved Oxygen and Illumination on the Behaviour of Roach (*Rutilus rutilus* (L.)), Bream (*Abramis brama* (L.)) and Perch (*Perca fluviatilis* (LL.)) 187

BRAGG, ARTHUR N. A Theory of the Origin of Spade-Footed Toads Deduced Principally by a Study of Their Habits 178

BROADHURST, P. L. Analysis of Maternal Effects in the Inheritance of Behaviour 129

CARR, ARCHIE & HIRTH, HAROLD. Social Facilitation in Green Turtle Siblings 68

CATLETT, ROBERT H. An Evaluation of Methods for Measuring Fighting Behaviour with Special Reference to *Mus musculus* 8

CHIANG, H. C. Ecology of Insects Swarms. I. Experimental Studies of the Behaviour of *Anarete near felti* Pritchard in Artificially induced Swarms (Cecidomyiidae, Diptera) .. 213

COWEY, A. *see* WEISKRANTZ, L.

EWING ARTHUR W. Body Size and Courtship Behaviour in *Drosophila melanogaster* 93

FREE, J. B. The Stimuli Releasing the Stinging Response in Honeybees 193

GORDON, JOHN G. The Relationship between Rumination and Frequent Feeding 16

GROSS, C. G. *see* LOVELL, M. R. C.

GROSSLIGHT, JOSEPH H. & HARRISON, PAUL C. Variability of Response in a Determined Turning Sequence in the Meal Worm (*Tenebrio molitor*): An Experimental Test of Alternative Hypothesis 100

GUITON, PHILIP. The Influence of Imprinting on the Agonistic and Courtship Responses of the Brown Leghorn Cock 167

HARRISON, PAUL C. *see* GROSSLIGHT, JOSEPH H.

HAUBRICH, ROBERT. Hierarchical Behaviour in the South African Clawed Frog, *Xenopus laevis* Daudin 71

HINDE, L. A. *see* KAUFMAN, I. C.

HINDE, R. A. *see* WARREN ROSLYN P.

HIRTH, HAROLD *see* CARR, ARCHIE.

HOYES, P. A. *see* SMITH, F. V.

JAMES, H. *see* ABERCROMBIE, BARBARA.

KAUFMAN, I. C. & HINDE, R. A. Factors Influencing Distress Calling in Chicks with Special Reference to Temperature Changes and Social Isolation 197

KING, JOHN A. Swimming and Reaction to Electric Shock in Two Subspecies of Deermice (*Peromyscus maniculatus*) during Development 142

CONTENTS

LOVELL, M. R. C., GROSS, C. G. & WEISKRANTZ, L. A Note on the Effects of Gymnemic Acid on Taste Perception 31

MANNING, AUBREY. Effects of Artificial Selection for Mating Speed in *Drosophila melanogaster* 82

MICHELS, KENNETH M. *see* WEAVER, LELON A.

MITCHELL, RODGER. Behaviour of the Larvae of *Arrenurus fissiconis* Marshall, A Water Mite Parasitic on Dragonflies 220

RATNER, STANLEY C. Effect of Learning to be Submissive on Status in the Peck Order of Domestic Fowl 34

ROBERTSON, K. G. *see* ALABASTER, J. S.

ROWELL, C. H. FRAZER. Displacement Grooming in the Chaffinch 38

ROWELL, THELMA E. Maternal Behaviour in Non-maternal Golden Hamsters (*Mesocricetus auratus*) 11

SIEGEL, H. S. & SIEGEL, P. B. The Relationship of Social Competition with Endocrine Weights and Activity in Male Chickens 151

SIEGEL, P. B. *see* SIEGEL, H. S.

SEXTON, OWEN J. & STALKER, HARRISON D. Spacing Patterns of Female *Drosophila paramelanica* 77

SMITH, F. V. & HOYES, P. A. Properties of the Visual Stimuli for the Approach Response in the Domestic Chick 159

STALKER, HARRISON D. *see* SEXTON, OWEN J.

TULLOH, N. M. Behaviour of Cattle in Yards. I. Weighing Order and Behaviour before Entering Scales 20

TULLOH, N. M. Behaviour of Cattle in Yards. II. A Study of Temperament 25

WARREN, ROSLYN P. & HINDE, R. A. Roles of the Male and the Nest-Cup in Controlling the Reproduction of Female Canaries 64

WEAVER, LELON A. & MICHELS, KENNETH M. Methodological Factors Affecting the Formation of Learning Sets by Rats 4

WEISKRANTZ, L. & COWEY, A. A Device for Measuring Food Motivation in the Monkey .. 1

WEISKRANTZ, L. *see* LOVELL, M. R. C.

BRIEF COMMUNICATIONS

CARLISLE, D. B. Intertidal Territory in Fish 106

MADGE, D. S. The Behaviour of Free-Living Mites as Affected by Humidity (*Acarina: Oribatoidea*) 108

MEAD, A. P. A Response of the Albino Rat to Red Light 225

RAMSAY, A. OGDEN. Behaviour of Some Hybrids in the Mallard Group 104

PROCEEDINGS OF THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR 109, 227

PROCEEDINGS OF THE SECTION OF ANIMAL BEHAVIOR AND SOCIOBIOLOGY (ECOLOGICAL SOCIETY OF AMERICA AND THE AMERICAN SOCIETY OF ZOOLOGISTS) 118
240

BOOK REVIEWS

BOLTON, W. Poultry Nutrition 123
Blood Groups, British Medical Bulletin, Vol. 15, No. 2 122
COLES, R. Development of the Poultry Industry in England and Wales 123
GOLDBERG, H. S. Antibiotics: Their Chemistry and Non-Medical Uses 121
LADYGINA-KOTS, N. N. Razvitiye psikhiki v protsesse evolyutsii organismov (Development of mentality in the process of the evolution of organisms) 243
LUKE, L. P. & SILVER, ALLEN. Aviaries, Birdrooms and Cages 123
MAYFIELD, HAROLD. The Kirtland's Warbler 243
MEYERRIECKS, ANDREW J. Comparative Breeding Behavior of Four Species of North American Herons 124
TANNER, J. M. (Ed.). Stress and Psychiatric Disorder 124
THURMER, TERESA E. Pet Chihuahua 121
VOISIN, A. (Translated by CATHERINE HERRIOT). Grass Productivity 122
WATMOUGH, W. The Cult of the Budgerigar 121
Bulletin 177 of the Ministry of Agriculture, Fisheries and Food. Machine Milking 123
A Journal of the British Veterinary Association. Research in Veterinary Science 122
British Medical Bulletin Vol. 16. Antibiotics in Medicine 121

This journal is copyright. It may not be reproduced by any means, in whole or in part, without permission. Applications with regard to reproduction should be addressed to the Publishers.

PRINTED IN GREAT BRITAIN
BY WELLINGTON PRINTERS
WELLINGTON, SOMERSET.

A DEVICE FOR MEASURING FOOD MOTIVATION IN THE MONKEY

By L. WEISKRANTZ and A. COWEY
Psychological Laboratory, University of Cambridge

The present report describes a device that has been found useful in the measurement of monkeys' strength of motivation for food reward. The selection of any technique, of course, depends upon the specific questions being asked by the experimenter. For our work we wanted a technique that did not require lengthy preliminary training of the animal and that permitted rapid shifting from one food to another. It had to be a reliable and rugged device, and, if possible, inexpensive. Finally, it had to be a "valid" device in the sense of supporting other parallel observations of motivational strength and in the additional and more interesting sense of generating lawful relationships.

Currently available techniques did not answer our requirements. The use of rate of occurrence of an operant response, such as lever pressing, and the latency of response (or force exerted) in a runway both require fairly extensive preliminary training; also, they do not permit rapid shift from one food to another as long extinction periods are generally required even when food is entirely withheld. In both, the animal is clearly dependent upon his memory of past reward as the reward is not present at the initiation of a response, so that response strength is, as it were, always at least one trial behind. The use of a shock barrier over which the animal must travel (using strength of shock as the dependent variable) can be criticized on the grounds that shock itself changes the general motivational state of the animal in a diffuse and often unpredictable manner (because, among other reasons, of an interaction with degree of food deprivation). The amount of food consumed until satiation, and the rate of eating, are unsatisfactory because the former permits only a very limited sample of behaviour for a given deprivational state, the latter because it probably does not vary sufficiently widely; and both suffer from not permitting rapid shifts from one food to another.

The device (Fig. 1) that was finally evolved is one in which a small piece of the food is placed on a skewer (A) attached to a trolley out of reach of the animal and in such a position that the food is clearly visible to the animal. The animal can pull the trolley to him by pulling on a string (B) attached to the trolley. Two response measures are available: the latency of response after an opaque screen between the animal and the apparatus is raised (we also measure the time required to attain the food once the string-pulling response is initiated); and the force exerted in pulling. The latency is measured quite reliably with an ordinary stop-watch, but it would be a simple matter to make such a measurement automatic by means of microswitch stops and a polygraph or some other suitable recording device. The force exerted is measured in arbitrary units directly upon a scale within the trolley. It would be a simple matter to convert these arbitrary units to grams of force by using suspended weights to shift the trolley; since we are interested only in changes in direction of motivation, the arbitrariness of the units is of no concern.

The device used to measure force is a simple dietary spring balance (C), (Salter Dietary Balance, No. 18D) the base mounted vertically on the back wall of the trolley. To it is attached a brass bar (D) weighing 175 gm. where the pan of the balance is normally mounted. When the trolley is pulled, a certain force must be applied to overcome the inertia of the system; the opposing force compresses a spring which pushes a "slave" indicator (E) on the scale. The indicator is mounted so that it measures the maximum excursion of the scale during a pull. Thumbscrews (F) permit the friction of the slave indicator to be altered. After each trial, the experimenter lowers the opaque screen, reads the slave indicator, and returns it to zero, ready for another trial. In order to obtain values of force within the range of the scale, we have found it necessary to require the animal to overcome, in addition to the inertia of the trolley itself, the restraint exerted by a Terry Clip (G) that embraces a horizontal bar (H) fixed on the trolley.

To ensure that the friction of the slave indicator is appropriately adjusted, a simple calibration device is employed. It consists of a tube (J) fixed to a heavy compression spring placed within a brass tube (I). A slot is cut in both tubes so that a sheet metal trigger (K) will maintain the spring compressed in a fixed position. When the trigger is pulled up, the spring is unloaded and the tube (J) strikes the

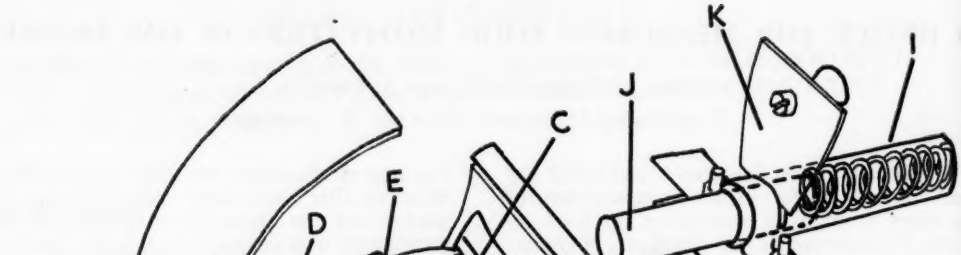


Fig. 1. For identification of lettering see text.

trolley with a constant force. The slave indicator can then be read. The friction thumb screws are adjusted so that the slave indicator gives the same fixed reading from session to session. In actual practice it is only rarely necessary to make this adjustment to the friction thumb screws.

The device is designed to fit into the widely used Wisconsin General Testing Apparatus, which already incorporates appropriate opaque screen and one-way vision screen. Generally we have given 20 trials per session which, with a moderately desirable food, occupies about 10 minutes total duration. In our situation the trolley is 60 cm. distant from the animal when the opaque screen is raised.

By means of a simple addition to the apparatus, it is possible to study extinction of the string-pulling response. The extinction device locks the trolley into position, and yet permits each attempted string pull to activate a microswitch. The current through the microswitch can then be led to a cumulative recorder (through an impulse shortner) and/or to a polygraph. The interest of using this technique for the study of extinction lies in the fact that the food reward is continuously visible to the animal. When, for example, one wishes to study extinction in animals who are suspected to have an impairment in immediate memory, the extinction curve produced in this situation will be more "pure" than the conventionally produced extinction curve. We have, for this reason, used the device to study extinction in monkeys with frontal cortex resections.

The device has been found to be quite satisfactory in the following respects. First, the latency measure has been found, with deprivation and type of food held constant, to be quite stable and reliable. The median latency does not change significantly within a session or from session to session. This assertion can be made with some confidence as a considerable body of data has been collected using the latency of response to bits of apple as a standard baseline.

Secondly, there is little question, once an animal has learned to recognise a food visually, that the visual presentation of the food exerts

a control over the response that is little contaminated by the animal's past experience with other foods in the situation. It has frequently been found that a food (such as tinned corned beef) which an animal has sampled and treated as undesirable will not yield even one further response by the animal; after a number of presentations of corned beef a piece of apple will yield a rapid response.

Thirdly, we feel that the latency measure derived from the situation possesses validity. Three experimenters testing independently have noted (our gross observations during each trial are always recorded on the data sheets) that the latency correlates quite well with subjective impressions of "eagerness" of the animal and the manner in which the animal treats the food once it is secured—i.e. whether he nibbles it, discards it, or gorges it. Also, while the matter has not yet been thoroughly investigated, latency appears to correlate reasonably well with the deprivational state of the animal. More importantly, it has yielded functional relationships that carry considerable theoretical significance for the analysis of the process by which new foods are gradually added to a monkey's repertoire of acceptable foods. In Fig. 2 for example, it can be seen that the effect of repeated testing with a new food gradually tends to delay the point at which the animal stops pulling in the food.

Preliminary analysis suggests that the measure of force, while quite reliable, does not vary consistently as latency varies. It looks as though monkeys come to pull with a fairly standard force if they pull at all. But as the force data have not yet been analysed in sufficient detail, it would be premature to rule it out as a valid measure of motivational strength. It would, of course, be of some interest if it were established that force does not vary with latency, as many current behavioural models would predict that it should.

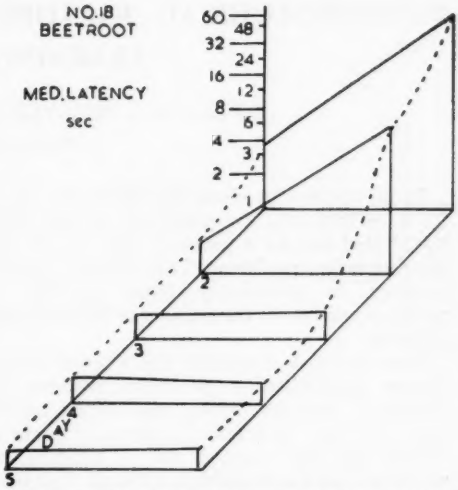


Fig. 2. The effect of repeated testing with a new food (beetroot). Twenty trials were given daily, and the medians of the first ten and the second ten trials are plotted for each of five days. It will be seen that the last ten trials of day one produced a median of 60 seconds (which was the longest interval allowed an animal). On successive days the curves become flatter and lower, indicating an approach to stable and rapid responding throughout the whole session.

In summary, a device has been described that possesses both reliability and validity as a measure of motivational strength for food by the monkey. It is very inexpensive and simple in construction, and appears to possess properties not generally found in other currently available techniques.

METHODOLOGICAL FACTORS AFFECTING THE FORMATION OF LEARNING SETS BY RATS

BY LELON A. WEAVER, JR.* AND KENNETH M. MICHELS
Purdue University, Indiana

In an attempt to assess the ability of rats to form learning sets, Koronakos & Arnold (1957) tested pied rats on a series of eight oddity-type discrimination problems. They found a general increase in proficiency from problem to problem in terms of the number of trials to reach criterion.

Since the task presented was a series of five-choice discrimination problems wherein the "correct" stimulus display was pitted against four identical "incorrect" displays, it might be argued that for many, if not all animals, the problems did not constitute different discrimination tasks in any sense comparable to those used in traditional learning set studies.

The present study was designed to explore some of the factors that might influence learning set formation. More specifically, these experiments were designed to elaborate further the results of Koronakos & Arnold (1957) through the use of different apparatus and procedures as well as with stimuli equated for brightness. Also to be compared was the relative efficiency of two-choice and four-choice stimulus presentation.

Method

Apparatus

All problems were presented in a four-choice discrimination apparatus. It consisted of a restraining box 12 in. × 12 in. × 12 in., painted flat black, in the front wall of which were four apertures, 2 in. × 2 in., backed by stimulus doors. A food-well was located immediately outside each door. An opaque guillotine screen mounted immediately in front of the stimulus doors could be lowered to prevent a view of the doors. A clear screen 4 in. in front of the opaque screen allowed a view of the stimulus display but prevented approach to the doors except when raised.

Each of the stimulus doors was securely hinged to a horizontal bar above the aperture by means of hooks such that it swung away from this opening when nosed by the animal subjects. A latching arrangement was provided so the "incorrect" doors could not be opened. All doors could be easily detached and shifted to any of the openings. The doors were cut from clear plexiglas on the back of which were fastened the discrimination patterns and background. The patterns were cut from black construction paper and mounted on white paper. They were illuminated from behind by 0·75 foot-candles.

The stimulus patterns were equated for area within each problem to control for brightness between correct and incorrect stimuli. Pairs of positive and negative stimuli used in all phases of the study are shown in Plate I.

Subjects

Twenty-two hooded rats, 90-100 days of age when introduced to the discrimination apparatus, served as subjects. They were divided into three groups: six were used in Experiment 1; nine in Experiment 2; and seven in Experiment 3.

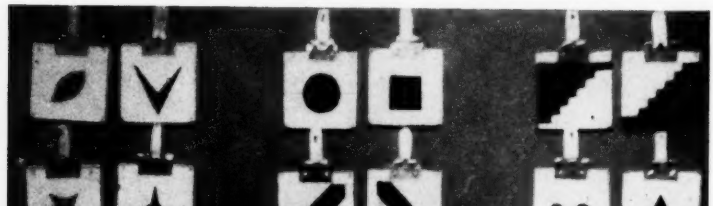
Procedure

At about three months of age the animals were placed on restricted food intake (10 grammes daily) and habituated for approximately 10 days to the apparatus. Habituation involved familiarization with the test box and training in the operation of translucent stimulus doors to retrieve food pellets.

The test procedure was as follows: The animal was placed in the test box, and while guillotine screens were down the stimulus doors were attached, food-wells baited, and the incorrect doors latched. The opaque screen was raised and the subject was allowed 10 seconds to view the stimulus display. Finally, the transparent screen was raised. If an incorrect response occurred, the opaque screen was immediately lowered to prevent correction, followed by the clear screen. If a correct response occurred, the screens were lowered after the animal had retrieved the pellet. The stimulus doors then were rearranged for the next trial. Observation of this process was prevented by the opaque screen. The location of the correct door was determined by a random sequence restricted to insure equal

*Now at the College of Medicine, University of Vermont.

PLATE I



The positive and negative stimuli for all phases of the study. In the four-choice experiments the negative stimulus was triplicated.

occurrence at all apertures. Approximately 10 seconds intervened between trials. The animals remained in the apparatus until the daily run of 25 trials was completed.

Experimental Design

Three experiments comprised the present study. In the first, the animals were run 25 trials per day on a series of ten, four-choice problems to a criterion of 13 correct out of a daily run of 25 trials (significant at the ·01 level) for two out of three days. An arbitrary cut-off point of 400 trials was decided on should an animal fail to reach criterion, at which time the next problem began. Each problem involved a correct pattern and three identical incorrect patterns. The sequence of problems was randomized for each animal.

In the second experiment the animals were tested on nine four-choice problems for 100 trials each. These began after the animals had learned a common training problem on the trials-to-criterion procedure used in the first study. The training problem selected was randomly chosen from the ten problems of Experiment 1 and this was used for all animals. The remaining nine problems were then used with the sequence being determined by a Latin square.

Immediately following completion of the tenth problem, the two outside doors were occluded and four two-choice problems were presented for 100 trials each.

The third experiment was run in reverse to the second. The training problem (two-choice, trials-to-criterion but with maximum of 1,000 trials) was followed by the ten, 100 trial, two-choice problems. These in turn were followed by four, 100-trial, four-choice problems. Initially there were nine animals in this group but two failed to learn the training problem in the maximum number of trials allowed.

Results

In Fig. 2 are summarized the results of the three experimental procedures where per cent. correct responses for each problem in sequence is presented. Since the second and third experiments first involved a training problem, the first problem for Experiment 1 is omitted to make the curves more comparable for the three groups.

In Experiment 1, where the animals were run to a criterion, there was a progressive increase in the per cent. correct responses reaching asymptote just about 85 per cent. for the last three problems. This difference among problems in sequence is significant beyond the 0·01 level (see Table I).

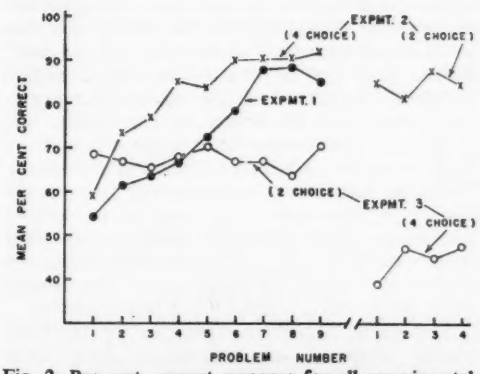


Fig. 2. Per cent. correct response for all experimental groups of animals on all problems following the training problem. In Experiments 2 and 3 the transfer performances of the group are presented on the right hand side of the figure.

Table I. Summary of Analyses of Variance for the Three Experiments.

Experiment	1	2	3
df	9	8	8
$F = \frac{\text{Trial blocks}}{\text{Residual}}$	13·03**	8·76**	0·61

**Significant at 0·01 level.

Essentially the same results were obtained in the second experiment except that the progressive increase from problem to problem reached asymptote sooner and at a slightly higher level, i.e. 90 per cent. correct immediately following the fifth problem. The sequence effect in the analysis of variance was significant beyond the 0·01 level in support of this change in performance.

The apparent difference between the curves for Experiments 1 and 2 is a function of the trials-to-criterion technique used in Experiment 1 which influences the upper limit of correct responses in the early stages of learning.

When the animals of Experiment 2 were tested on four, two-choice problems, only a slight drop in performance was observed. This slight decline was found to be a probable function of one of the problems selected which proved to be a significantly more difficult one than any of the

others (variance due to problems is significant at the 0·01 level). When the results on this problem are removed from the data, the animals' performance is at 90 per cent. correct on the first problem, 89 per cent. on the second, 92 per cent. on the third, and 94 per cent. on the fourth.

In the third experiment where the animals were first tested on two-choice discrimination problems, no significant improvement from problem to problem was noted over the series used for testing. Although some learning took place within the 100 trials of each problem, as reflected by the means being above the chance level, there was no progressive improvement.

The effect of initial experience in the two-choice situation on subsequent four-choice learning may be seen also in Fig. 2. There is a marked drop to near the chance level for four choices and only a limited improvement over the problems used.

In an attempt to evaluate the effect of method (two-choice vs. four-choice), the performance on the training problems was compared for animals in Experiments 2 and 3. These results may be summarized by saying that there was no overlap in performance between the two groups; that is, the slowest learning animal in the four-choice group was superior to the fastest learning animal in the two-choice group.

Table II summarizes the performance of three groups of animals on the same training problem. Each group was run to the same criterion of learning (performance significant at the 0·01 level for any two of three successive blocks of 25 trials) or were terminated at the 40th block. It is apparent that there is a marked difference in the Blocks to Criterion column. The trend which is evident for Group II and absent for Groups III and IV requires no further comment.

Discussion

The data of the initial experiment support those of Koronakos & Arnold (1957) in demonstrating that rats can form learning sets. The improvement from problem to problem, however, is much more rapid in the present studies (Experiments 1 and 2) which may be taken as support for the apparatus and methodology employed. First of all, the apparatus was designed to maximize the spatial contiguity of the stimulus, response and locus of reward. Furthermore, the stimuli were confined to 2×2 inch panels which are smaller than those used in most discrimination experiments with rats. The overall size of the display of correct and incorrect stimuli was also reduced through the use of smaller patterns. The clear restraining screen not only imposed an "inspection" period but also reduced further the size of the visual images. These factors appear to have contributed to the more rapid improvement in learning by reducing the magnitude of locomotion and head movement necessary for visual examination and comparison of the characteristics of the stimuli.

Since the first experiment and the first phase of the second experiment involved learning to discriminate a correct stimulus from three identical incorrect stimuli, it could be argued that the various problems merely provided additional practice on the "oddity" problem. However, the high degree of transfer to the two-choice situation in the second experiment indicates that the animals had learned to discriminate form *per se*.

When two-choice problems are used initially, as in the third experiment, improvement from problem to problem is so slight as to be not apparent over the number of problems used here. The animals adopt such stereotyped patterns as place responses and the resulting 50 per cent. reinforcement ratio appears to be sufficient to maintain the response. When the animals were shifted to four-choice problems essentially no change in performance occurred. The animals

Table II. Summary of Performance of Animals on the Same Training Problem to Some Criterion of Performance.

Group	Method	No. of Sub's.	Blocks to Criterion	Blocks without significant learning		Blocks with significant place error	
				1st hf.	2nd hf.	1st hf.	2nd hf.
II	4—C	9	99	52	33	15	6
III	2—C	10	342	171	165	56	50
IV*	2—C	9	334	166	167	106	116

*This group was run to check the results obtained on Group III and was discontinued at the end of the training problem.

continue to operate at the near chance level (now 25 per cent.). The stereotyped response appear so well established that little improvement occurs over the four problems. In the four-choice situation such responses disappear quite rapidly and the learning of the appropriate responses is facilitated.

The data reported in Table II support the stereotype interpretation. The blocks containing a significant place error account for a large proportion of the blocks which show no significant learning and also show no evidence of diminishing in the second half of the trial blocks. In two animals in Group III, a significant place response occurred in 36 and 38 out of 40 blocks of trials.

This study demonstrates the need for more critical appraisal of apparatus and methodology if ultimate capacities are to be determined and compared as is the intent of most comparative psychologists. It appears that smaller stimuli and the concurrent decrease in size of the overall display, an enforced "inspection" period, and early training on multiple choice problems markedly facilitates interproblem learning.

Summary

Three groups of hooded rats were run in three experiments involving visual discrimination problems. In the first experiment rats run to criterion showed significantly increasing proficiency over ten four-choice problems. The animals of the second group also improved in learning ability when tested on 100-trial, four choice problems reaching 90 per cent. correct responses by the fifth problem. When these animals were then tested on four two-choice problems, only a slight decrement occurred. Animals tested on two-choice problems followed by four-choice showed no such improvement.

The results are interpreted to indicate rats do form learning sets and under appropriate procedures do so to a remarkable level.

REFERENCES

Johnson, J. I., Jr. & Michels, K. M. (1958). Learning sets and size effects in visual discrimination learning by raccoons. *J. comp. physiol. Psychol.*, **51**, 376-379.

Koronakos, C. & Arnold, W. J. (1957). The formation of learning sets in rats. *J. comp. physiol. Psychol.*, **50**, 11-14.

Harlow, H. F. (1949). The formation of learning sets. *Psychol. Rev.*, **56**, 51-65.

Hays, K. J., Thompson, R. & Hayes, C. (1953). Discrimination learning set in chimpanzees. *J. comp. physiol. Psychol.*, **46**, 99-104.

Miles, R. C. & Meyer, D. R. (1956). Learning sets in marmosets. *J. comp. physiol. Psychol.*, **49**, 219-222.

Shepard, W. O. (1957). Learning set in preschool children. *J. comp. physiol. Psychol.*, **50**, 15-17.

Warren, J. M. & Baron, A. (1956). The formation of learning sets by cats. *J. comp. physiol. Psychol.*, **49**, 227-231.

Accepted for publication 1st *August*, 1960.

AN EVALUATION OF METHODS FOR MEASURING FIGHTING BEHAVIOUR WITH SPECIAL REFERENCE TO *Mus musculus*

By ROBERT H. CATLETT

Department of Zoology, University of California, Davis, California

The purpose of this report is to introduce a new measure of fighting behaviour—accumulated attacking time—and to evaluate it along with two standard measures of aggressiveness, fighting response latency and number of attacks.

Although a relatively small amount of time is spent fighting, its importance in controlling population density is agreed upon by a number of workers in the field. Brown (1953) concluded that fighting, associated with establishment and maintenance of social hierarchy, was one of the factors limiting the growth of caged populations in his study, and suggested that this may apply to natural environments. Deaths, as a result of fighting, have been reported by Crew & Mirskaia (1931) and Retzlaff (1938). Southwick (1955) reported that when fighting intensity reached one fight per hour per mouse in each of his large pens, litter mortality was excessive, and population growth was impaired. The total importance of aggressive behaviour, of which fighting behaviour is a major component, is thoroughly treated ecologically by Collias (1944) and Allee (1951). Scott (1958) presented the major concepts of aggressive behaviour, and emphasized its importance in relation to human populations as well as wild animal populations. From this, we may conclude that fighting behaviour may be of some biological significance among certain animals in caged populations. It is difficult to relate the importance of fighting to natural populations, but it may in certain cases have a biologically significant effect particularly within populations where a social hierarchy is established by fighting.

When studying fighting behaviour, the investigator must choose an index of aggressiveness. Various methods of measuring fighting behaviour have been proposed by a number of workers in the field. Early studies by Yerkes (1913) and Utsurikawa (1917) employed rating scales to indicate the amount of fighting. This involved a qualitative evaluation of each animal's performance before a rating value could be assigned. In much of the later work, measures of the actual amount of fighting behaviour have been eliminated, and the dominant-subordinate relationship has been used. The positive-negative response, which refers to an animal either engaging in a fight (positive) or not engaging in a fight (negative) has also been employed. Beeman (1947) used the ratio: "Attacks/Tail rattles plus attacks" to evaluate fighting behaviour among groups of mice. Fredericson (1949) proposed using the fighting response latency which is the time elapsed between placing of mice together and their first fight. Another widely used measure is the number of attacks one animal makes on another. These attacks may be defined as the biting, wrestling, and chasing which occurs between the animals. Studying *Mus musculus*, Brown (1953) indirectly measured attacking intensity by counting the number of wounds an animal received. King (1957) employed both number of attacks and fighting response latency in his study of *Mus* and *Peromyscus*.

Method

A recent study was designed to determine the effect of mating on dominant male house mice (Catlett, 1958). Subjects for the two experimental runs were male house mice (*Mus musculus* L.). Twenty-four mice were used in experiment I, forty in experiment II. The parental male stock of the subject were wild mice four or five generations removed from the original feral stock captured in or near Colorado Springs, Colorado. The parental females were of the white Swiss strain. In experiment I, the mice ranged from forty-five to one hundred and twenty days in age. In experiment II the age range was between forty-five and sixty-two days. The mice were isolated from the litter at 30 days, and were kept isolated until the beginning of each experiment.

The twenty-four males in Experiment I and the forty males used in Experiment II were divided randomly into pairs. In Experiment I, each pair of the twelve pairs of mice was allowed to fight for a five minute period daily for ten consecutive days. In Experiment II the procedure was the same as in Experiment I, but the time was extended to thirteen days. In both

experiments the same two mice or pair were allowed to fight each other each day. It was noted in both experiments that very shortly after the mice were placed together one mouse was easily identified as dominant in that he showed superior fighting ability. Very little resistance was offered by the subordinate mouse after this dominant-subordinate relationship was established. During the five periods, three measures were made: fighting response latency, number of attacks, and accumulated attacking time. Accumulated attacking time may be defined as the total or accumulated time that a dominant mouse spent chasing, biting, wrestling or striking the subordinate mouse.

To evaluate the reliability of the three measures, correlations were determined for odd and even day scores. To evaluate the association between measures, Pearson product-moment correlations were made. During Experiment II, the fighting response latency was not recorded due to the physical limitations of the experiment.

In testing or measuring animal responses, differences in output or scores are expected over periods of time. The reliability of a measure is difficult to determine since learning, age change, and various physiological processes may be affecting the animal's performance. By finding the coefficient of reliability for scores in this study it was hoped that some indication of the difference over a period of time could be established. The reliability of any test is measured by the similarity of results attained when the same test is repeated. The reliability of scores in this study was determined by simply calculating the coefficient of correlation between odd and even day scores for all three measures for both experiments. Values obtained are averages for Experiments I and II since the differences were extremely slight, not more than 0·03 maximum. The increase in the reliability coefficient was computed by the Spearman-Brown formula

$$r_n = \frac{nr11}{1+(n-1)r11}$$

where $r11$ = the coefficient of reliability for the original test

r_n = the increased reliability coefficient due to repetition

n = number of subjects.

More simply explained, the degree of reliability is a measure of the degree of similarity of scores in a two-day period.

Results and Discussion

The increased reliability coefficient, r_n gave the following average values: Number of attacks, r_n=0·96; accumulated attacking time, r_n=0·98; fighting response latency, r_n=0·99. P values were <0·01 for all three, and the correlations are noticeably high. The statistically highly significant values for r_n in all three cases indicate that the measures are all highly reliable. The question then arises as to the degree of association between measures (Table I). All the correlations coefficient are high, and statistically highly significant; the P value was <0·01. The highest value for r is between accumulated attacking time and number of attacks in Experiment I. The lowest value of r is between accumulated time and fighting response latency for Experiment I (note the negative correlations as would be expected). The absolute value still

Table I. Pearson Product-Moment Correlations Among Measures for Experiments I and II.

Experiment	Measures	*df*	*r*	*P*
I	Accumulated attacking time Number of attacks	59	0·84830	<0·01
I	Number of attacks Fighting response latency	59	—0·63870	<0·01
I	Accumulated attacking time Fighting response latency	59	—0·54817	<0·01
II	Accumulated attacking time Number of attacks	129	0·55690	<0·01

exceeds the value necessary for statistical significance at the 0·01 level.

When fighting behaviour is measured by counting number of attacks, it is difficult to decide what constitutes a single attack. The decision concerning when an attack begins and when it ceases is easier to make. Therefore, I believe that accumulated attacking time is perhaps the easiest and most profitable measure to use when recording fighting behaviour since mice spend a sizeable part of each fight chasing, biting or wrestling one another. In recording number of attacks, a conflict which may begin with chasing or biting is counted as one attack. The accumulated attacking time for this encounter which is taken at the beginning, i.e. first chasing or biting, may vary from 0·15 to 0·5 second. Accumulated attacking time is measured as a continuous variable while number of attacks is measured as a discrete variable. By using a measure which is a continuous variable, fractions of a period may be included. Fractions cannot be included when using a discrete variable as is the case with number of attacks.

If measuring fighting behaviour, accumulated attacking time may be used to strengthen the judgment concerning fighting behaviour. If the animals spend considerable time during one attack or fight, it may help to time this attack since duration is well worth measuring. The disadvantage of using the fighting response latency, as compared with the other measures, is the difficulty encountered in getting mice into an equidistant position before the fight begins; its advantage is the minimization of injury to combatants since mice can be separated after the initial encounter.

Conclusion

It can be seen that fighting behaviour may be measured by the accumulated attacking time, number of attacks, or the fighting response latency, and comparable results are obtained due to the high degree of association among these measures. All three of these measures are desirable when more information is desired. When an experiment limits the use of more than one of these measures the investigator may be assured that he is measuring one behavioural pattern which is closely associated with the other two. Statistically and biologically one would expect this association to hold true in a high percentage of cases since the amount of fighting is based on certain fixed physiological mechanisms. If these mechanisms are upset, or if animals of a different kind are used, the association between measures may be altered.

Summary

1. In Experiment I and Experiment II, 12 pairs and 20 pairs, respectively, of male house mice were measured for fighting behaviour output for five minutes daily. Experiment I ran ten days, Experiment II, thirteen days.

2. The dominant mouse of each pair was measured for accumulated attacking time, fighting response latency and number of attacks.

3. Increased reliability coefficients were statistically significant for all three measure, $P<0{\cdot}01$.

4. Product-moment correlations between measures were significant, $P<0{\cdot}01$, indicating a high degree of association.

5. All three measures were considered desirable in the evaluation of fighting behaviour.

REFERENCES

Allee, W. C. (1951). *Co-operation among animals*. Rev. ed. New York: Henry Schuman.

Beeman, Elizabeth A. (1947). The effect of male hormones on aggressive behavior in mice. *Physiol. Zool.*, **20**, 373-405.

Brown, Robert Z. (1953). Social behaviour, reproduction, and population changes in the house mouse (*Mus musculus* L.). *Ecol. Monogr.*, **23**, 217-240.

Catlett, Robert H. (1958). The effect of mating experience on fighting behaviour of dominant male house mice. (*M.A. Thesis, Colo. College*).

Collias, N. E. (1944). Aggressive behaviour among vertebrate animals. *Physiol. Zool.*, **17**, 83-123.

Crew, F. A. E. & Mirskaia, L. (1931). The effects of density on adult mouse populations. *Biol. Gen.*, **7**, 239-250.

Fredericson, E. (1949). Response latency and habit strength in relation to spontaneous fighting in C57 black mice. *Abst. Anat. Rec.*, **105**, 509.

King, John A. (1957). Intra- and interspecific competition of Mus and Peromyscus. *Ecology*, **38**, 355-357.

Retzlaff, E. C. (1938). Studies in population physiology with albino mice. *Biol. Gen.*, **14**, 238-265.

Scott, J. P. (1958). *Aggression*. Chicago: The University of Chicago Press.

Snedecor, George W. (1957). *Statistical methods*. Amer.: Iowa State College Press.

Southwick, Charles H. (1955). Regulatory mechanisms of house mouse populations: social behavior affecting litter survival. *Ecology*, **36**, 627-634.

Utsurikawa, N. (1917). Temperamental differences between outbred and inbred strains of the albino rat. *J. anim. Behav.*, **7**, 111-120.

Warne, M. C. (1947). A time analysis of certain aspects of the behaviour of small groups of caged mice. *J. comp. physiol. Psychol.*, **40**, 371-387.

Yerkes, R. M. (1913). The heredity of savageness and wildness in rats. *J. anim. Behav.*, **3**, 286-296.

Accepted for publication 31*st August*, 1960.

MATERNAL BEHAVIOUR IN NON-MATERNAL GOLDEN HAMSTERS

(Mesocricetus auratus)

By THELMA E. ROWELL

Introduction

It is usually assumed that lactating female mammals will show only appropriate maternal behaviour towards their young. In a colony of Golden hamsters, however, it was found that normal mothers occasionally attacked and ate their own young, and though usually good foster mothers, sometimes attacked strange pups (Rowell, 1960). Another common assumption is that, with the exception of man, mammals show maternal behaviour only when influenced by the hormone balance (induced naturally or experimentally) appropriate to the lactating female. A number of authors, however, have described maternal behaviour shown by normal untreated rodents of all ages and degrees of experience and both sexes (Nelson & Leblond, 1936; Horner, 1947; Frank, 1952; Klein, 1956).

Dieterlin (1959) made some incidental observations on maternal behaviour in non-lactating Golden hamsters. He says that males living with lactating females show an "inhibition of biting" towards young less than fifteen days of age. He describes one male retrieving and brooding his mate's one-day old litter. Mixed results were obtained with non-maternal females: some tolerated a pup placed in their nest, others killed and ate it. Beniest (1958) has recently made a thorough study of this phenomenon in the laboratory mouse, and found that maternal responses as strong as those of lactating females were shown by all categories of non-lactating animals.

During a series of tests in which female hamsters with litters between three and four weeks old were offered young pups, it was observed that if her young found the test pup before the mother did, they would carry it to the nest, lick and brood it, thus showing many of the maternal responses she might herself show. This phenomenon was investigated further, to find out how widespread mternal responses in non-lactating Golden hamsters were, and in what circumstances they occurred.

The observations described here make an interesting comparison with those of Beniest because hamsters and mice have rather different ways of life, the former being a solitary animal, while the latter lives in a social group.

I. Tests on Adults

Material

The adult animals in the colony live in individual cages with a floor area of about two square feet. They are given bedding with which they make a nest, and have an abundant supply of varied food including milk. Young animals live with their mothers for four weeks and then in groups for a further two or three weeks.

Methods

Tests were all made in the first four hours of darkness, which is the period of maximum activity for the hamster. (The colony was kept in artificial light adjusted so that darkness began at midday and lasted ten hours). Animals were offered pups between three and eleven days old and their reactions towards them recorded. Two ways of presenting the test pups were used:

(i) the pup was placed on the floor of the cage and the occupant was allowed to come across it there.

(ii) the animal was taken out of the cage and given food to put in her pouches, while the pup was placed in the nest. After an interval she was returned to her cage, and found the pup in her nest.

Behaviour Seen in the Test Situation

In the first situation, the response of a lactating hamster to a pup of this age would be to pick it up in her mouth, carry it to her nest, put it with the rest of her litter, lick it, and then either to brood the litter, or to go out to the place where she found the pup and "look for more". This series of activities is called retrieving, since its normal function would be to collect her own straying litter. A lactating female in the second situation would probably appear not to notice the strange pup, or she might sniff it a little. She would empty her pouches on to the food pile and settle down to brood.

The least maternal response possible was for the test pup to be treated as prey, that is to be

killed and eaten without hesitation. Intermediate responses between these extremes were less common: pausing a few seconds before killing; ignoring the pup; sniffing and licking it all over the body, but especially in the shoulder region (which are intention movements of picking up to retrieve); carrying it about (but without damaging the skin). Another pattern, often difficult to distinguish from the sniffing and licking which is an intention movement for retrieving, is following the pup as it crawls about, licking its ano-genital region. It indicates that the response of the animal being tested is partly sexual, the behaviour being also seen in the early stages of precopulatory behaviour of the male.

Results of Tests on Adults

1. *Males*. Eight males were tested. Three killed and ate pups. Five sniffed and licked, mainly in the ano-genital region, carried it to the nest, and sat over the pup, but not in the brooding position.

2. *Females*. Thirty-three tests were made on solitary adult females. These were:

15 tests on pregnant animals at all stages from fifteen days to less than one day before parturition.

18 tests on non-pregnant animals of which 5 were nullipares.

All these females will be considered together, because with the numbers of results available useful comparisons of the effect of breeding status cannot be made.

In 20 of the tests the pups were found on the floor of the cage. All were eaten at once when found.

In the other 13 tests the pups were found in the nest: five of these were eaten at once.

Four were eaten after a pause in which they were licked.

One was licked until it fell out of the nest, whereupon it was eaten.

Three were accepted and mothered.

These results include three females which were tested twice, once with a pup on the cage floor and once with a pup in the nest. One of them ate both pups. The other two ate the one found on the cage floor, but mothered the one found in the nest (both possible orders of testing were used).

Two of the pups which were accepted were left with the females. One lived for three days, then died apparently of starvation. The other was older when adopted, and survived, though becoming very thin before it could feed itself adequately. The foster mother was offered strange pups, on the cage floor after the adoption, and she retrieved them normally. Neither of these females apparently gave any milk in response to their foster pups' suckling attempts.

To summarize, adult females that are not lactating usually eat young pups. Pups found in the nest box, however, have some chance of being accepted and mothered, unlike those found elsewhere in the animal's territory.

II. Tests on Juveniles

Materials

Pups of thirty-one families were used in an attempt to discover when maternal behaviour developed, how long it lasted (adult females having been found to treat pups as prey) and if it was affected by the social situation in which the animal lived.

Methods

In tests on juveniles, the test pup (1-8 days old) was always placed on the floor of the cage, and observations continued until the older pups lost interest in it, or for up to twenty minutes.

When the litter to be tested was living with its mother, she was taken out of the cage during testing, because she would usually monopolise the test pup herself otherwise.

Similarly, if one of the litter monopolised the test pup it was sometimes taken out of the cage, so that the response of the others could be seen.

18 litters lived with their mothers (two of these were single pups).

6 litters were taken from their mothers at eighteen to twenty days, and kept in their family groups.

7 litters were split, and some pups left with the mother while others were handreared, kept in isolation, or in unisexual groups.

4 litters were tested daily over a period of one or two weeks. Another 4 were given single "spot tests" to act as controls for a learning effect occurring in other groups. The remainder were tested at intervals of about four or five days, when test pups were available.

Behaviour in the Test Situation

The types of behaviour observed were for the most part the same as those seen in the adults. The young animals might retrieve the test pup and brood it in the nest; often this behaviour was not completed either because the test pup was too heavy to be successfully manoeuvred through the nest entrance, or because of inter-

ference from interested litter-mates who tried to take it away and carry it themselves. Often the test pup was picked up and dropped, or just licked and mouthed in the shoulder region, before they lost interest. Non-maternal responses included a cursory sniff followed by ignoring the pup; a startle response on coming across it, sometimes followed by cautious snapping at it; and eating it.

The "maternal" behaviour of the pups, though composed of the same behavioural elements as that of the lactating female, looks different. It has many of the attributes of play activity (Beach, 1945): the patterns are often not complete but are broken off suddenly, or change to grooming or fighting with siblings. The young animal gives an impression of "not knowing what to do next" which is very unlike the purposeful impression given by the lactating female.

Results of Tests on Juveniles

There was no observable differences in the type and amount of maternal behaviour shown by male and female pups.

Development of Retrieving Response

Licking and mouthing of younger pups was first seen at fifteen days. In one litter, no maternal behaviour was shown at sixteen days, though they sniffed and licked the pup. The next day the test pup was picked up and dropped, and complete retrieving occurred on day eighteen. All ten litters tested at this age had shown some maternal response by day nineteen. It seemed that the appearance of the retrieving patterns was dependent only on attaining the physical strength necessary to pick up an object—perhaps a quarter of the retrieving pup's own weight.

Until they are twenty-eight days old, juveniles usually take the test pup to the nest. Often it is carried in the mouth, sometimes three-to-five day old test pups take hold of the belly or genital organs of an investigating juvenile with its mouth and it is then always dragged to the nest. I have never seen a test pup attacked when attached in this way, although its victim is obviously uncomfortable, grunts and tries to run away.

After twenty-eight days the amount of time spent with the test pup decreases, so that though it may be retrieved, it is usually being ignored by the end of a fifteen minute test. It is also frequently carried, not to the mother's nest in which they were reared, but to a corner of the cage where the litter usually plays.

Litters living with their mothers, having stopped showing appreciable amounts of maternal responses, begin to attack and eat test pups. The first sign of this change was often the appearance of a startle response in the first juvenile to find the pup. It would then often approach again cautiously and snap. A few days before, the same animal may have retrieved a similar pup. Ten litters living with their mothers were followed until they began to eat test pups (and once they had eaten one they continued to eat all further test pups). The average age at which eating first occurred was thirty-seven days (range of 29-47 days); two families, however, had shown no aggression at fifty-four and forty-nine days respectively, when tests were discontinued.

Effect of Absence of Mother

Groups without an adult, on the other hand, continued to tolerate test pups, usually licking them a little and occasionally retrieving until over fifty days (oestrous cycles begin at about six weeks in the females). This effect of the mother increasing the aggressiveness of the litter was well shown by one family, which began to attack test pups on day 29. The pups were then divided into three groups, a group of three males and one of three females were taken from the mother, and two males and three females were left with her. On the next day all groups showed some aggression. On day 33 and subsequently, the pups remaining with the mother continued to attack test pups, while the other two groups showed retrieving behaviour.

Presence of Siblings

Young animals without siblings, whether with their mother or alone, behave differently from those in groups. They are much less active, and spend long periods crouching motionless in corners. They respond more slowly to test pups than do group animals, and retrieve less frequently, but are also slower to become aggressive. One pup which was reared alone by a foster mother was still retrieving when her littermates with their mother had become aggressive. A male and a female pup which were isolated at three weeks also retrieved after the rest of their litter had begun to eat pups. The female first attacked a test pup on day forty-eight.

Nine females from litters living without their mothers were put into separate cages between day forty-five and fifty-five, and tested two days later. (Males were not treated in this way since solitary adult males also showed maternal be-

haviour, and no change was predictable). All but one attacked the test pup, although before isolation they had shown maternal behaviour. In two cases females remaining in the groups could be tested at the same time, and they continued to tolerate the test pups. When they were isolated after this control test, they too became aggressive to test pups.

Handrearing

This is technically difficult, but three pairs of pups were reared from about eleven days. They retrieved as well as, and as soon as, their siblings remaining with the mother.

Age of Test Pups

New-born pups offered to females at all stages of lactation in another test series were found to have a much lower chance of being treated maternally than pups two or three days old (40 per cent. of new-born pups offered were rejected but only 21 per cent. of two-day olds). Juveniles showed the same differentiation. New-born pups were offered on six occasions. Three were killed, and one elicited only cursory inspection. The four litters involved were offered a total of fifty-seven older pups at other times, and of these three were attacked, and twelve were accorded general interest only.

To summarise, young hamsters begin to show maternal behaviour towards very young pups as soon as they are strong and active enough to do so. They retrieve pups well until about four weeks, then show lessening interest up to about five weeks. Pups living with their mother begin to kill and eat very young pups at this stage. In groups without their mother, toleration, with occasional retrieving of young pups, continues after the females become sexually mature. Females from these groups that are isolated begin to kill and eat pups. Like lactating females, juveniles are less maternal to new-born pups than to older pups.

Discussion

It is apparent that the young hamster pup can produce different responses from older animals, and evoke behaviour appropriate to conspecific young, to prey (like many other rodents, hamsters are omnivorous) and, to a lesser extent, to sex partner. The question of what conditions, external and internal, determine which response is elicited cannot yet be answered in full, and it is perhaps unlikely that any one explanation will be found to cover all examples: even lactating females do not always show maternal responses to their own pups. The animals which were offered young pups represented a very wide range of age, experience and reproductive status in both sexes. It is possible that all the animals which showed maternal behaviour were secreting lactation hormones, but this is unlikely and if true would throw doubt on the usual interpretation of the occurrence, function and specificity of these hormones, which is not justifiable in the light of physiological evidence. Certainly the animals were not apparently lactating. A simpler explanation would be that sensory stimuli from young pups elicited maternal behaviour from all members of the species. Beniest's results with mice would fit this explanation, since nearly all her animals showed maternal behaviour towards strange young mice almost as strongly as did lactating females. The picture for the Golden hamster, however, is more complex. This is probably associated with the solitary habit of the adult hamster, and its aggressiveness towards other hamsters, compared with the relatively peaceful communally living mouse. Two factors emerge as being of particular importance in determining behaviour towards young.

1. *Territory*. Sexually mature females living alone killed and ate pups, but those living in a group, and therefore having no individual territory, remained tolerant towards them. Adult males tested were all sexually active. Such animals appear to have territorial rights only with respect to other males, and usually do not attack even anoestrous females entering their cages. In the complete family group aggrese sion by the litter towards test pups begin before sexual maturity in the females, at about the timthe family might normally be expected to break up under natural conditions. This may be correlated with the increased aggressiveness of the mother towards her offspring at this stage, as she begins to treat them as territorial rivals.

2. *The Nest*. In non-lactating solitary adults females, which are the group most aggressive to pups found in their cages, pups found in the nest itself are sometimes given maternal care. The nest of a hamster, and especially the female, is enormously important in its life. At least eighty per cent. of its time is spent there, food is taken there to be eaten, and most activities are oriented and influenced by it. The sudden appearance of pups in the nest is partly comparable to the situation at parturition. During

normal birth a pregnant female, very aggressive towards strange pups, becomes a lactating female, who will probably accept them and mother them, but then also the appearance of the pups *in the nest* is partly conditional for their acceptance (Rowell, 1960 b).

Thus it seems that, when considering maternal behaviour in the Golden hamster, a complex of factors other than the hormone balance of the "mother" and sensory stimuli from the "baby" must be considered, which are at first sight irrelevant to the immediate situation. The place of the encounter in relation to the living space of the animal, and the animal's relationship with its own living space and with other animals may all affect its response to conspecific young, There are also important species differences. Those between the hamsters and the mouse have already been mentioned; the rat, which has a similar life history, is frequently stated (e.g. Wiesner & Sheard, 1933) to ignore young pups except when lactating. The possibility of differences between strains within a species has also not been explored in this particular context. It is clear that generalizations about the factors eliciting and controlling maternal behaviour in rodents can be made only with the greatest caution.

Summary

Non-lactating Golden hamsters were offered young pups, and their reaction towards them observed.

Adults and juveniles of both sexes were tested. All groups would show maternal behaviour, in particular, "retrieving" of young. Solitary adult females would treat maternally only those pups they found actually in their nest.

Juveniles began to retrieve younger pups as soon as they were strong enough, and when living in groups without their mother continued to retrieve or tolerate pups after sexual maturity. Living with their mother they began to attack pups at about five weeks, before the females were mature. When group-living females were isolated, they also began to be aggressive to pups.

The results are compared with published data on rats and mice.

Acknowledgment

This work was carried out while the author held a research studentship from the department of Scientific and Industrial Research.

REFERENCES

Beniest, E. (1958). Analyse du comportement dit maternel chez la souris. *Monogr. francaises de Psychol.* 1. Paris.

Dieterlin, F. (1959). Das Verhalten des Syrischen Goldhamsters. *Z. Tierpsychol.*, **16,** 47-103.

Frank, F. (1952). Adoptions versuche bei Feldmäusen. *Z. Tierpsychol.*, **9,** 145.

Horner, B. E. (1947). Paternal care of young mice of the genus *Peromyscus*. *J. Mammal.*, **28,** 31-36.

Klein, M. (1956). Aspects biologiques de l'instinct reproducteur dans le comportement des Mammifères. *L'instinct dans le comportement des animaux et d'homme*, Paris: Masson.

Leblond, C. P. & Nelson, W. O. (1937). Presence d'instinct maternel sans stimulation hormonales. *C.R. Soc. Biol.*, **124,** 1064.

Rowell, Thelma E. (1960a). On the retrieving of young and other behaviour in lactating Golden hamsters. *Proc. zool. Soc., Lond.*, **135,** 265-282.

Rowell, Thelma E. (1960b). The family group in Golden hamsters: formation and break-up. *Behaviour* (in press).

Wiesner, B. P. & Sheard, N. M. (1933). *Maternal behaviour in the rat*. Edinburgh: Oliver & Boyd.

Accepted for publication 10*th October*, 1960.

THE RELATIONSHIP BETWEEN RUMINATION AND FREQUENT FEEDING

By JOHN G. GORDON

Rowett Research Institute, Bucksburn, Aberdeen

Introduction

Gordon & Tribe (1952) have shown that 22 young growing sheep produced greater body-weight gains through increased efficiency of food utilization when offered their daily ration in eight small feeds than they did when given the same quantity and quality of food in one large feed. Over 18 weeks a total gain of 298 lb. was made, of which 196 lb., or 65·8 per cent., were due to frequency feeding.

Precisely similar effects do not seem to have been noted in the literature. However, Cuthbertson & Munro (1939) found that changing the human dietary regime from 8 to 2 meals per day brought about a transitory loss of nitrogen, and Moore, Hoffman & Berry (1945) found that cod-liver oil fed to cattle in one meal reduced milk fat production but when the same amount was fed in 12 small doses the milk fat was not affected.

While discussing possible reasons for an increased food efficiency in sheep Gordon & Tribe (1952) postulated four theories, one of which was:

> "It is possible that the length of time spent ruminating by the animal under the two systems of management may be different and might, by the consequent differences in mechanical action upon the food, result in difference in digestibility. Continuous observations were made on the ruminating behaviour of four sheep, two from each group over a 72-hour period. The total time spent ruminating by the two frequently fed sheep was 2534 min., whereas the two singly fed sheep spent 3483 min. ruminating."

In order to investigate this further the following experiment was carried out.

Experimental

Four Blackface wether hogs were divided into two groups, A and B, each of two animals so that the groups were as nearly equal in body-weight as possible. Each animal was then fed a diet of 640 g. stock concentrates and 400 g. chopped hay daily. (The concentrates were made up as follows: yellow maize meal 4, crushed oats 1, wheat bran 1, white fish meal ½ and linseed cake meal ½, parts by weight). The amounts fed were such as to allow for both maintenance and growth. Water was offered *ad. lib.* but no salt licks were given. The animals were individually housed in recording cages, placed so that one group could not see the other.

During the first part of the experiment, which lasted for a period of nine weeks, from June 3rd to August 4th inclusive, group A was fed eight times daily at approximately hourly intervals between the hours of 9.30 a.m. and 5.15 p.m. On each occasion one-eighth of the total ration was given, *i.e.* 80 g. concentrates and 50 g. chopped hay. Group B received its daily ration as one large feed at 9.15 a.m. For the second period the treatments were reversed, group B being given the frequent treatment and group A fed once daily. The second period was also of nine weeks from August 5th to October 6th inclusive. The animals were shorn on July 24th and the fleeces weighed. (Shearing was delayed because no "rise" appeared in the wool.) The body weights of the animals were recorded at frequent intervals throughout the experiment.

Recordings of jaw movements were made from all four sheep during each experimental period—a continuous paper recorder was used (Gordon, 1955). After a period of four weeks had elapsed, to allow the animals to become accustomed to the system of feeding, two animals—one from each pair—were recorded simultaneously; immediately after this the other two were recorded. In Period 1 these records were for six days, *i.e.* six days from one pair, followed by six days from the other. In Period 2 only four-day records were made as it was then considered that four days were adequate.

Results and Discussion

Table I shows how, in terms of body weight, the animals reacted to frequent feeding. (To simplify matters, the weights at the end of Period 1 include fleece weights, but those in Period 2 are shorn weights). During Period 1 group A, which was fed frequently gained more than did group B, fed the same amount of food as one meal. In Period 2 group B, fed frequently gained more than group A, fed once daily. However, in actual fact, group A gained only 1 lb. as the

Table I. Effect of Frequency of Feeding on Body Weights (lb.) of Sheep.

Period	Group	A		B	
	Sheep no.	568	494	569	504
1*		*Frequent feeding*		*Single feeding*	
	Beginning	90	77	93	72
	End	97	87	99	76
	Gain	7	10	6	4
	Group gain	17 (Frequent)		10 (Single)	
	Fleece weight	10	7	7	6
2*		*Single feeding*		*Frequent feeding*	
	Beginning	87	80	92	70
	End	97	86	101	87
	Gain	10	6	9	17
	Group gain	16 (Single)		26 (Frequent)	
Gain due to frequent feeding		1		16	

*Period 1, weights including fleece; Period 2, shorn weights.

result of frequent feeding but group B gained a total of 16 lb., as the result of this same regime; this is of the order found in the previous experiment (Gordon & Tribe, 1952). Sheep 568 is responsible for the small effect in group A because it gained 3 lb. more on the once-a-day feeding than on frequent feeding. Therefore, 3 out of the 4 sheep showed a strong positive effect of frequent feeding. This effect might have been greater if the sheep fed one large meal per day had eaten all their food within a short period of time. All four sheep ate all but a small amount of their food, consisting only of hay, within two hours of feeding. Sometimes all was consumed in that time; but in general there was sufficient left to lead to short periods of eating

Table II. Effect of Frequency of Feeding on the Behaviour of Sheep.
Behaviour of Group A.

Sheep No.			568								494							
Period treatment		Day	Idling hr.	Idling min.	Eating hr.	Eating min.	Drinking hr.	Drinking min.	Ruminat'g hr.	Ruminat'g min.	Idling hr.	Idling min.	Eating hr.	Eating min.	Drinking hr.	Drinking min.	Ruminat'g hr.	Ruminat'g min.
1	Frequent feeding	1	12	2	2	49	0	2	9	7	12	19	2	47	0	5	8	49
		2	12	17	3	2	0	3	8	38	13	23	2	45	0	12	7	40
		3	13	25	3	49	0	2	6	44	11	11	4	8	0	11	8	30
		4	14	2	2	44	0	2	7	12	10	56	3	53	0	2	9	9
		5	10	32	4	22	0	2	9	4	11	1	4	37	0	0	8	22
		6	16	34	3	1	0	1	4	24	12	33	3	32	0	1	7	54
	Mean per day		13	8	3	18	0	2	7	32	11	54	3	37	0	5	8	24
2	Single feeding	1	15	10	2	59	0	1	5	50	10	39	4	9	0	0	9	12
		2	15	22	3	1	0	0	5	37	11	44	4	34	0	5	7	37
		3	14	24	3	6	0	0	6	30	15	53	1	10	0	3	6	54
		4	13	52	3	18	0	0	6	50	11	46	3	39	0	6	8	29
	Mean per day		14	42	3	6	0	0	6	12	12	31	3	23	0	3	8	3

later in the day. However, this does not explain the failure of sheep 568 to gain more when fed frequently, since its behaviour was not markedly different from that of the other sheep.

The total times spent in ruminating are shown in Tables II and III.

Table II shows that this particular sheep 568 ruminated for a distinctly longer time per day in Period 1, when fed frequently than in Period 2, when fed once a day. This suggests that the effect of frequent feeding was negatived by long chewing times. Sheep 494 also ruminated for a little longer when fed frequently but it reacted favourably to frequent feeding. In Table III sheep 504 ruminated much less in Period 2 while fed frequently than in Period 1 when fed once a day, and it gained much more body weight while on frequent feeding than it did on single daily feeds. Sheep 569 showed half-an-hour more rumination when fed eight times a day than when fed once a day. These figures are in disagreement with Gordon & Tribe (1952) quoted above, and yet 504, which showed the greatest positive effect of frequent feeding—it gained 13 lb. extra as compared with a loss of 3 lb. for 568 and gains of 4 lb. and 3 lb. for 494 and 569—showed a decrease of almost an hour in daily cudding time when fed frequently. Although this is less than half the order of difference quoted above, it is nevertheless a large one.

The only other important point emerging from these tables is that in every case frequent feeding led to a longer total time, from 12 to 23 minutes more, spent in eating. This may produce more efficient digestion, one possibility being that the flow of saliva may be a function of the time spent eating.

In order to examine the ruminations further the data in Table IV were compiled from further analyses of the records. The total numbers of periods of rumination are greater during frequent feeding in group A, but in group B this is not the case. Likewise the total number of boli is greater during frequent feeding in group A, and in sheep 569 in group B, but this does not correspond with the effect of the two treatments on all the animals. Thus these factors appear to be unimportant. However, on examining the "cyclic rate" *i.e.* the time taken from the beginning of one bolus to the beginning of the next, it is noticed that the rate is always slower on the single feeding regime than it is on the frequent one, averaging 64 seconds on single feeds and 61 seconds on frequent feeding, for all four animals.

Since the cyclic rate is virtually the rate of contraction of the reticulum (Gordon, 1955), it may be linked with the overall state of motility, and thus the digestive processes, of the stomach and small intestine, since these parts share a common parasympathetic motor innervation from the tenth cranial nerves (*vagi*) (Lenkeit, 1933). Increased motility may bring about a more rapid passage of material from the reticulo-rumen into the omaso-abomasum (Wester, 1930), and decrease carbohydrate loss in the reticulo-rumen and the effect of frequent feeding may be accounted for in this way.

Table III. Effect of Frequency of Feeding on the Behaviour of Sheep.

Behaviour of Group B.

Sheep no.			569								504							
Period treatment		Day	Idling hr.	Idling min.	Eating hr.	Eating min.	Drinking hr.	Drinking min.	Ruminat'g hr.	Ruminat'g min.	Idling hr.	Idling min.	Eating hr.	Eating min.	Drinking hr.	Drinking min.	Ruminat'g hr.	Ruminat'g min.
1	Single feeding	1	16	14	1	51	0	2	5	53	13	58	2	6	0	2	7	54
		2	16	4	1	24	0	2	6	30	14	0	2	7	0	1	7	52
		3	15	36	1	33	0	1	6	50	13	35	2	5	0	0	8	20
		4	14	50	1	17	0	2	7	51	13	44	1	50	0	1	8	25
		5	15	21	1	27	0	2	7	10	13	50	2	17	0	1	7	52
		6	17	51	2	8	0	1	4	0	12	30	2	46	0	1	8	43
	Mean per day		15	59	1	37	0	2	6	22	13	36	2	12	0	1	8	11
2	Frequent feeding	1	16	15	1	30	0	1	6	14	13	14	2	1	0	0	8	45
		2	14	43	1	50	0	10	7	17	15	27	2	39	0	0	5	54
		3	15	14	2	13	0	1	6	32	13	43	2	58	0	0	7	19
		4	13	59	2	7	0	1	7	53	14	4	2	42	0	0	7	14
	Mean per day		15	3	1	55	0	3	6	59	14	7	2	35	0	0	7	18

Table IV. Other Factors Involved in the Effect of Frequency of Feeding in Sheep.

Group		A*								B*							
Sheep no.		568				494				569				504			
Period	Day	‡ Total per'ds	Total boli	Boli per period	† Cyclic rate	‡ Total per'ds	Total boli	Boli per period	† Cyclic rate	‡ Total per'ds	Total boli	Boli per period	† Cyclic rate	‡ Total per'ds	Total boli	Boli per period	† Cyclic rate
1	1	26	517	20	64	17	442	26	72	14	399	28	53	25	469	19	61
	2	17	495	29	63	12	355	30	78	14	411	29	57	23	449	20	53
	3	16	415	26	59	14	469	34	65	13	446	34	55	17	489	29	61
	4	26	448	17	58	13	458	35	72	16	519	32	54	20	485	24	62
	5	34	569	17	57	14	420	30	72	15	489	32	53	25	472	19	60
	6	20	299	15	53	20	395	20	72	12	258	22	56	19	519	27	60
	Mean	23	457	20	59	15	423	29	72	14	420	30	55	22	481	22	61
2	1	14	330	24	64	10	432	43	77	13	453	35	50	16	496	31	64
	2	12	338	28	60	12	348	29	79	17	489	29	54	13	351	27	60
	3	14	380	27	62	9	304	34	82	15	461	31	51	15	463	31	57
	4	18	413	23	59	12	393	33	78	12	529	44	54	13	438	34	60
	Mean	15	365	25	61	11	369	34	79	14	483	35	52	14	437	31	60

*Period 1: A frequent, B single. Period 2: B frequent, A single. ‡ of rumination.

†Average no. of seconds from beginning of one bolus to beginning of next.

Summary

1. An attempt was made to relate rumination to the effect of giving the same total amount of food in small frequent feeds as opposed to giving it in a single feed in increasing the efficiency of food utilization by sheep.

2. In three of the four sheep used there was a positive effect.

3. Total rumination time, the number of periods of rumination and the total number of boli were found to bear no relationship to the increased efficiency of food utilization.

4. It was found that the rate of regurgitation of boli was more rapid in all sheep when frequently fed, and it is postulated that this may reflect a general increase of motility of the foregut, of secretion and of digestion.

REFERENCES

Cuthbertson, D. P. & Munro, H. N. (1939). The rôles of total dietary carbohydrate and of surfeit carbohydrate in protein metabolism. *Biochem. J.*, **33**, 128-142.

Gordon, J. G. (1955). Rumination in the sheep. Thesis: Aberdeen University.

Gordon, J. G. & Tribe, D. E. (1952). The importance to sheep of frequent feeding. *Brit. J. Nutr.*, **6**, 89-93.

Lenkeit, W. (1933). Neuere Ergebruisse der Verglichenden Physiologie der Verdamung der Saugetiere. *Ergebn. Physiol.*, **35**, 573-631.

Moore, L. A., Hoffman, G. T. & Berry, M. H. (1945). The effect of two different methods of feeding cod-liver oil on fat test in milk. *J. Dairy Sci.*, **28**, 161-166.

Wester, J. (1930). The rumination reflex in the ox. *Vet. J.*, **86**, 401-410.

Accepted for publication 26th *September*, 1960.

BEHAVIOUR OF CATTLE IN YARDS. I. WEIGHING ORDER AND BEHAVIOUR BEFORE ENTERING SCALES

By N. M. TULLOH
School of Agriculture, University of Melbourne

Introduction

Irrespective of his specialist interest, the man who carries out research involving live animals must inevitably study to some extent the behaviour of his experimental subjects. Indeed it frequently happens that such behaviour observations enable the researcher to make a more critical interpretation of his results. A knowledge of the effect that an experimental treatment may have on an animal's behaviour is often essential before a suitable experimental design can be made. Just as an appreciation of the importance of behaviour assists the worker in various disciplines, so the behaviour observations, usually recorded incidentally by the man in other specialist fields, have often proved of interest to the behaviourist. The observations recorded by Braude (1948) on pigs, and by Walker (1950) on calves, are examples of this reciprocity of interest.

The observations now reported were carried out on an experimental herd of beef cattle which was being used primarily for a study of physiological processes of growth and development. For this purpose it was necessary to weigh cattle regularly and when doing this it was noticed on several occasions that the animals appeared to arrive at the scales in similar order. It was therefore arranged to determine whether this was in fact the case, and, if so, whether an animal's weighing order was related to one of its characters such as sex, weight, and horned or polled condition. The behaviour when entering the scales also differed between animals, yet it seemed to be constant for an individual. The opportunity was also taken to study this aspect of behaviour.

Method

A herd of 18 male and 18 female horned Hereford cattle was grazed on irrigated pastures at the Melbourne and Metropolitan Board of Works sewage disposal Farm, Werribee, Victoria. These animals were born in August-September, 1957, and observations on behaviour commenced on January 26th, 1958, when the mean age of all calves was 156 days. On February 3rd, nine of the bulls were castrated and nine of the heifers were dehorned. The remaining bulls were castrated on April 29th (mean age 241 days). Half of the herd was weaned on June 2nd (mean age 275 days) and the remaining calves were weaned on July 21st (mean age 324 days).

Animals were allocated to these various treatments after considering birth date, birth weight, growth rate and sex.

The experimental animals normally grazed with other cattle of similar age, making a total herd size of 80 cattle. When the herd was yarded, unwanted animals were removed by drafting. The experimental animals were then moved into a large holding yard near the scales. Groups of 5 to 10 animals were then moved into a small yard just behind the scales. From there an animal could be driven along a short narrow race and held by sliding gates until required for weighing. A plan of the yards is given in Fig. 1. When the experiment started, the herd had been weighed by this method on only one previous occasion some two months before. Dogs were never used when handling these cattle in the yards. Animals were weighed off grass at the rate of approximately one a minute, weighing normally starting at 0930 hours. As each animal was weighed its order of appearance in the range 1 to 36 was noted. This was called its "weighing order". The scheduled weighings when order was recorded, were as follows:

Period.	*Number of weighings*
I Pre-experimental period (January 26 to February 3)	4
II Period between dehorning, and castration of half the bull calves (February 3) and castration of remaining bull calves (April 29)	8
III Period between April 29 and weaning first half the herd (June 2)	5
IV Period between June 2 and weaning of remaining calves (July 21)	4

The behaviour of animals immediately before entering the scales was scored as follows:

Entry to Scales	*Score*
Without hesitation	1
Hesitantly, vocal encouragement necessary	2
Only if urged with cane, then enters easily	3
Difficult to get into scales	4

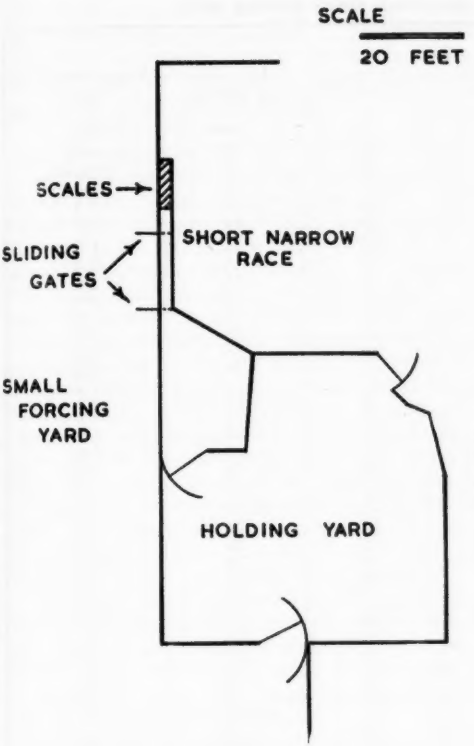


Fig. 1. Plan of cattle yards.

Behaviour immediately before entering the scales was recorded on eight occasions between May 26th and August 18th, 1958.

Results

Weighing Order

The mean weighing order for each animal in each of the periods I, II, III, IV and for all periods is given in Table I. A ranking test using Kendall & Babington Smith's (1939) coefficient of concordance gave the following results:

Period I	Ranking not significant
Periods II, III, IV	Ranking highly significant for each period ($P<0.01$).
All periods (i.e. throughout the experiment).	Ranking highly significant. ($P<0.01$).

The correlation between mean rankings for the various periods were calculated using Spearman's coefficient (as described by Kendall, 1943). They were as follows:

I —	II	0·29	(not significant)
II —	III	0·36	(significant, $P<0.05$)
III —	IV	0·58	(significant, $P<0.001$)
IV —	all periods	0·70	(significant, $P<0.001$)

It was thought that this weighing order may have been related to the experimental procedures imposed on the herd, and therefore the weighing order was compared with each of the procedures for each of the periods. Statistical tests showed that weight, sex, horned condition, and weaning were not related to mean weighing order. The data for body weight, sex and horned condition are shown in Figs. 2 and 3.

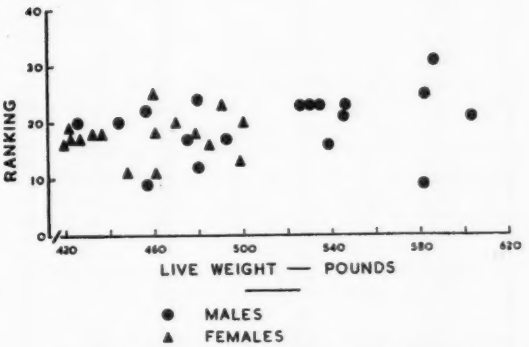


Fig. 2. Comparison of ranking (mean weighing order for all periods) and live weight at end of period IV.

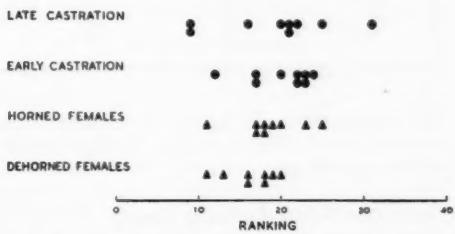


Fig. 3. Relation between ranking (mean weighing order for all periods) and effects of castration and dehorning.

There appeared to be some association of pairs of animals in the weighing order. On five occasions out of 23 (including two later weighing orders not included in the four periods mentioned above) animals 1099 and 1028 appeared together or separated by one other animal. Similarly, 1028 and 1058 appeared together or separated by one other animal on seven occasions. There was no association between 1099 and 1058 except on one occasion when 1099,

Table I. Weighing Order and Behaviour Immediately Before Entering Scales.

Animal	Mean weighing order					Mean behaviour score
	Period I	Period II	Period III	Period IV	All periods	
1047	12	7	13	6	9	2·4
1099	9	6	10	16	9	1·3
1072	13	7	12	10	10	missing
1003	9	14	4	17	11	1·9
1096	15	11	8	12	11	2·3
1062	13	16	5	10	12	1·5
1128	29	8	10	13	13	1·9
1024	17	13	18	17	16	2·3
1058	19	19	17	8	16	1·0
1098	12	21	17	11	16	1·0
1086	21	19	15	11	17	1·3
1012	18	19	14	17	17	2·3
1073	20	14	19	18	17	1·0
1065	20	24	7	15	17	1·0
1100	24	9	24	23	18	1·1
1059	20	17	19	18	18	1·5
1101	19	12	26	21	18	1·4
1093	17	16	21	21	18	1·4
1079	23	15	24	22	19	1·3
1094	19	18	19	23	19	1·1
1056	24	22	11	22	20	1·3
1082	18	22	13	26	20	1·0
1133	11	22	30	15	20	1·5
1027	19	23	18	18	20	1·3
1126	20	13	25	32	21	1·0
1028	20	29	15	17	21	1·1
1000	13	25	28	15	22	2·4
1125	20	19	28	25	23	1·4
1134	19	25	19	29	23	1·5
1090	28	25	19	19	23	1·6
1076	7	25	31	26	23	1·1
1095	26	27	23	15	23	1·5
1075	21	27	21	21	24	1·5
1060	20	29	21	23	25	1·1
1018	28	20	28	27	25	1·6
1092	28	31	33	29	31	1·1

1028 and 1058 all appeared together. These associations became obvious during Period III of the experiment.

Behaviour Before Entering Scales

The mean scores for behaviour immediately before entering the scales for 35 animals on eight occasions are given in Table I. Seven animals were entirely consistent in scoring "1" on each occasion. A χ^2 test showed that the mean score for behaviour before entering the scales for each animal was not related to its weighing order. There was a downward trend from 1·5 to 1·3 in the mean score for behaviour for all animals during the experiment. An analysis of variance showed that this downward trend was not significant. The mean score for all animals on all occasions was 1·4.

Discussion

When a few animals have to be separated from a herd of yarded cattle which is itself on the move, those standing or moving near an appropriate gateway are driven through by the stockmen. Animals appear to be moving at random in the milling herd and they may appear to be treated roughly and forced to move quickly. In spite of this treatment, the cattle used in this experiment managed to develop and maintain a significant weighing order. From an experimental point of view this is important in relation to loss of fill; that is loss of weight due to urination and defaecation whilst standing in the yards. Animals which appear early in a weighing order will weigh relatively more than they should, compared with those which appear late. Repeated weighings will not eliminate this ex-

perimental error. However, apart from loss of fill, as weighing order appears to be unrelated to factors concerning growth and development, it need not be considered when allocating animals to experimental groups.

No attempt was made to find the order of social dominance in this herd. However, Woodbury (1941) has suggested that "hook order" is largely determined by the size, shape and effectiveness of horns, whereas in dehorned cows "bunt order" is largely determined by an animal's strength and tenacity in pushing. Schein & Fohrman (1955) in their analysis of social dominance in a herd of dairy cattle have shown a good relationship between dominance and weight. On the basis of this evidence and the fact that weighing order appears to be unrelated to sex, weight or horned condition, it seems unlikely that weighing order is related to dominance. Schein & Fohrman (*loc. cit.*) also suggest that "the social position of each animal is probably determined at three to six months of age". Therefore it is probable that this herd was old enough to have developed an order of dominance before or during the experiment.

All animals were held in the yards until weighing was completed, and then they were returned as a herd to their grazing paddock; there was therefore no immediate reward after weighing. It is unlikely, then, that weighing order is conditioned by a reward factor.

It appears that weighing order is an order in the herd based on leadership which may not be related to social dominance, animals developing this leadership during a succession of similar experiences on each weighing day, namely, movements through yards, drafting and weighing. The evidence of Kilgour & Scott (1959) working with milking cows also suggests that leadership and dominance are poorly related.

The association of pairs of animals in the weighing order suggests that certain animals developed friendly relations with others during the experiment. In fact, some animals recognized as pairs in the weighing order were occasionally observed grazing together. "Friendly pairs" do not necessarily have similar mean weighing orders. For example the mean weighing orders (all periods) for 1099, 1028 and 1058 were 9, 21 and 16 respectively. 1099 (castrate male) and 1058 (female) appeared to have no regard for one another, but 1028 (castrate male) frequently associated with 1099 and 1058.

The pattern of behaviour immediately before entering the scales is not an effective measurement of temperatment because it was observed that some docile animals scored high or low, for behaviour immediately before entering the scales, as did some animals regarded as nervous. These observations on temperament have been continued on other cattle and will be reported in another paper.

Behaviour immediately before entering the scales was unrelated to weighing order. In this instance, it may have been strongly influenced by the steel ramp leading into the scales and the dark weighing cage which, except for the top and small inspection grills near the doors, was covered with sheet metal and painted black inside.

Summary

The observations reported in this paper concern the behaviour of 36 young Hereford cattle yarded for weighing at regular intervals.

During the experiment the cattle developed a significant weighing order which was unrelated to sex, weight, horned condition, or the effect of weaning. It is suggested that this weighing order is not related to social dominance, but represents another order of herd leadership. The practical importance of weighing order is discussed.

The behaviour of these cattle immediately before entering the scales was consistent for a number of individuals. It was not a satisfactory measure of temperament and appeared to be related to the design and installation of the scales.

Acknowledgments

The author wishes to thank the Reserve Bank of Australia (Rural Credits Development Fund) for financial assistance, the Melbourne and Metropolitan Board of Works for permission to use their cattle and their facilities, and particularly their staff for assistance with this work. The advice of Mr. T. Verhagen, Division of Mathematical Statistics, Commonwealth Scientific and Industrial Research Organization, and Mr. R. Jardine of the Victoria Department of Agriculture, on the statistical methods used in this paper is greatly appreciated.

REFERENCES

Braude, R. (1948). Some observations on the behaviour of pigs in an experimental piggery. *Bull. anim. Behav.*, **6**, 17-25.

Kendall, M. G. (1943). *The advanced theory of statistics.* Vol. I. London: Charles Griffin.

Kendall, M. G. & Babington Smith, B. (1939). The problem of *m* rankings. *Ann. maths. Stats.*, **10**, 275-287.

Kilgour, R. & Scott, T. H. (1959). Leadership in a herd of dairy cows. *Proc. N.Z. Soc. anim. Prod.*, **19**, 36-43.

Schein, M. W. & Fohrman, M. H. (1955). Social dominance relationship in a herd of dairy cattle. *Brit. J. anim. Behav.*, **3**, 45-55.

Walker, D. M. (1950). Observations on behaviour in young calves. *Bull. anim. Behav.*, **8**, 5-10.

Woodbury, A. M. (1941). Changing the hook order in cows. *Ecology*, **22**(4), 410-411.

Accepted for Publication 20*th September*, 1960.

BEHAVIOUR OF CATTLE IN YARDS. II. A STUDY OF TEMPERAMENT

By N. M. TULLOH

School of Agriculture, University of Melbourne

Introduction

Various authors have published opinions on the temperament of different breeds of cattle and generally this approach has been similar to that used by Kelley (1943) reporting observations on crosses between Zebus (*Bos indicus*) and British breeds (*Bos taurus*). He writes of them as follows:

"Zebu-British breed crosses are more difficult to handle than British breed animals. They have a 'reputation for touchiness', are regarded as 'lively'; in yards calves 'kick with accuracy and force', when leg roped for branding. . . . The quarter-bred Zebus have a better temperament than the half-breds . . . When drafting cattle, Zebu cross animals are more difficult to block at gateways than British breed cattle. All breeds of cattle are not equally placid. This is true even of British breeds. Among them, Shorthorns are probably the most phlegmatic, while Aberdeen Angus are possibly the most lively. When handled skilfully, however, all are very similar."

Some authors (Brownlee, 1950, 1954, 1957; Fraser, 1957a; Schloeth, 1956) have described behaviour patterns of cattle in considerable detail; for example, combat activity, self defence, challenge behaviour, fight or flight reaction, curiosity. However, in these papers behaviour patterns have not been related to temperament. Fraser (1957b) cites Parez (1953) as assessing temperament in bulls according to "strength", "balance" and "liveliness". Although Parez describes what he means by these terms, Fraser concludes that "The bulls forming the subject of the French work cannot be very representative". In his own study, Fraser has described six behaviour groups based on 79 bulls representing five British breeds and the Chillingham Wild White Cattle, but his classification is subjective and represents an anthropomorphic approach. Scott (1958) has investigated the inhibition of milk production as a function of temperament, and he has produced evidence that the two are related but his assessment of temperament is based on farmers' ratings of their own animals.

This paper reports the behaviour of beef cattle when handled in yards and temperament scores based on this behaviour.

Methods

This work was carried out at the Melbourne and Metropolitan Board of Works Farm, Werribee, Victoria, where the cattle were grazed on sown pastures irrigated with sewerage effluent.

The cattle used consisted of 72 animals, representing 12 steers and 12 heifers of each of the following breeds—Hereford (horned), Shorthorn (horned), and Aberdeen Angus (polled). These cattle were born during late August-September, 1957, and were selected at random from a herd of 180 calves. At the age of four months all bull calves were castrated and the Hereford and Shorthorn heifers were dehorned. The observations on behaviour were made incidentally to a comparative growth study of the three breeds involving weighing, coat sampling, skeletal, and other measurements which required the animals to be yarded once a month. Observations on behaviour commenced in mid July, 1958, when the mean age of all cattle was 320 days and ceased in June, 1959. However, as the animals were yarded regularly from birth onwards, they had opportunities to become accustomed to the procedures used on them before observations on behaviour began.

Steers and heifers were run in separate herds, but within a herd breeds were kept together throughout the experiment. After yarding a herd, the 36 animals were weighed according to the procedure described by Tulloh (1960). Each beast was then moved from a small forcing yard and through a narrow gateway (sliding gate) to a crush with a bail at the end of it. A plan of the forcing yard, crush and bail is shown in Fig. 1.

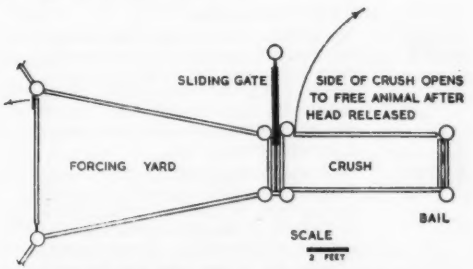


Fig. 1. Plan of forcing yard, crush and bail.

Reaction to handling (that is "behaviour" in this paper) was recorded on the following occasions: entering the scales, entering the crush, entering the bail and in the bail.

Behaviour was recorded in the following ways:

Entering the Scales or the Crush

Description	*Score*
Without hesitation	1
Animal hesitant, vocal encouragement necessary	2
Animal enters only if urged using cane, then enters easily	3
Difficult to persuade animal to enter	4

Entering the Bail

Description	*Score*
Moves towards bail and attempts to put head through on own initiative. (An animal which tries to get head through but fails because of trouble with horns is included here)	1
Animal hesitant, with vocal encouragement moves towards bail; head must be guided through, offers token resistance	2
Animal difficult to move towards bail, evades efforts to guide its head through, but resists for short period only	3
As in 3 above, but resistance strenuous and prolonged	4

In the Bail

Depending on the number of observations to be made on an animal and its reaction to them, it may have been in the bail from five to 25 minutes. During this time its behaviour was recorded. At the end of the experiment, descriptions of behaviour were summarised into temperament scores. The temperament scores were as follows:

Temperament	*Description*	*Score*
Docile	An animal which stands quietly in the bail, rarely moves except to raise or lower head; may lean forwards or backwards or against side of crush; animal is easily positioned for observations and is generally unperturbed by the whole procedure	1
Slightly restless	An animal which is generally docile, but moves frequently and will not remain positioned for more than a few seconds; flicks tail occasionally; blows quietly through nostrils. An animal which is stubborn but otherwise docile is included here	2
Restless	An animal which moves almost continuously, pulling or pushing on bail and pushing on sides of crush; stance is difficult to make observations on; flicks tail frequently, snorts; animal objects to having ear tag handled during identification; may be stubborn	3
Nervous	A restless animal which *quivers* when a hand is placed on its back, defaecates whilst in bail, animal may be stubborn	4
Wild	A restless animal which struggles violently; bellows and froths at the mouth; animal may be stubborn	5
Aggressive	A wild animal which attacks observers by kicking, or by attempting to butt them by lunging forward in bail during head measurements; animal may be stubborn	6

An animal was described as "stubborn" when it opposed attempts to move it. No attempt was made to score degrees of stubbornness; however, stubbornness is a poor indication of temperament because both docile and aggressive animals were stubborn at times. For this reason stubbornness was not considered important in the temperament classifications, except when an otherwise "docile" animal was classed as stubborn, in which case it was included in the "slightly restless" category.

All decisions on description of behaviour and on the allocation of temperament scores were made by the author.

The occasions on which behaviour was recorded are shown in Table I. It should be noted in this table, that almost twice as many observations were made on steers as on heifers.

Table I. Occasions on which Behaviour was Recorded.

Behaviour recorded	Number of occasions		
	Steers		Heifers
	Range	Mean	
Entering scales	3	3	3
Entering crush	5—6	5·8	3
Entering bail	4—5	4·5	3
In the bail (for temperament score)	5—6	5·5	3

Results

1. Behaviour Entering the Scales

The mean scores for all breeds and sexes when entering the scales are shown in Table II. The mean score for all animals was 1·9 and differences between breeds and sexes were not significant.

2. Behaviour Entering the Crush

The mean scores for all breeds and sexes when entering the crush are shown in Table III. The mean score for all animals was 1·8. An analysis

Table II. Mean Scores for Behaviour Entering Scales.

Breed	Scores					
	Steers		Heifers		All animals	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
Hereford	1·8	0·17	2·0	0·21	1·9	0·14
Angus	1·8	0·18	2·0	0·26	1·9	0·16
Shorthorn	2·0	0·22	1·7	0·19	1·8	0·15
All breeds	1·9	0·11	1·9	0·13	1·9	0·08

of variance showed highly significant differences between mean scores for breeds. Hereford scores were higher ($P<0·01$) than Angus and Shorthorn scores, but differences between Angus and Shorthorn scores were not significant. Sex differences were not significant.

Table III. Mean Scores for Behaviour Entering Crush.

Breed	Scores					
	Steers		Heifers		All animals	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
Hereford	2·0	0·07	2·1	0·16	2·1	0·08
Angus	1·6	0·05	1·7	0·12	1·7	0·08
Shorthorn	1·8	0·09	1·6	0·08	1·7	0·06
All breeds	1·8	0·06	1·8	0·08	1·8	0·05

A χ^2 test showed that there was no relation between scores for entering the scales and entering the crush, although scores were low for both activities.

3. Behaviour Entering the Bail

The mean scores for all breeds and sexes entering the bail are shown in Table IV. The mean score for all animals was 2·3. An analysis of variance showed that Hereford scores were significantly higher ($P<0·01$) than Shorthorn scores. Other differences between breeds and sexes were not significant. χ^2 tests showed that there was no relation between scores for entering the bail and entering the scales or the crush. However, t-tests showed that scores for entering the bail were significantly higher ($P<0·001$) than these other scores.

4. In the Bail (Temperament Scores)

The mean temperament scores for all breeds and sexes are shown in Table V. The mean

Table IV. Mean Scores for Behaviour Entering Bail.

Breed	Mean Scores					
	Steers		Heifers		All animals	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
Hereford	2·6	0·13	2·6	0·18	2·6	0·11
Angus	2·2	0·13	2·5	0·18	2·3	0·11
Shorthorn	2·3	0·16	1·9	0·15	2·1	0·11
All breeds	2·4	0·08	2·3	0·11	2·3	0·08

score for all animals was 2·2. An analysis of variance showed highly significant differences between mean scores for breeds. Hereford scores were lower ($P<0·01$) than Shorthorn scores, but not significantly lower than Angus scores. Angus scores were also lower ($P<0·05$) than Shorthorn scores. The difference between mean scores for sexes just failed to reach the 5 per cent. level of significance.

Table V. Mean Scores for Behaviour in Bail (Temperament)

Breed	Scores					
	Steers		Heifers		All animals	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
Herefords	1·5	0·05	2·0	0·11	1·7	0·10
Angus	2·2	0·23	2·2	0·16	2·2	0·19
Shorthorn	2·4	0·16	3·1	0·28	2·7	0·23
All breeds	2·0	0·14	2·4	0·20	2·2	0·11

Using χ^2 tests, temperament scores were compared with scores for entering the scales, the crush and the bail and there was no relation between them.

Mean temperament scores for all animals were graphed against live weights recorded in December, 1958, and are shown in Fig. 2. The mean live weight of all animals was 672 lb. Farmers would regard animals with temperament scores of "2 or less" as desirable and those with scores "greater than 2" as undesirable. By dividing the cattle into these two categories and at the same time dividing them according to live weights above or below the mean, a two by two contingency table was constructed. A χ^2 test on this table, using Yates' correction, showed a significant relation ($P<0·05$, $\chi^2=$

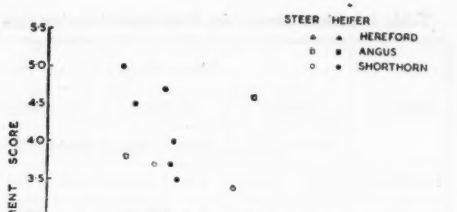


Fig. 2. Relation between mean temperament score and live weight for each animal.

4·66, v=1). between temperament and live weight.

Discussion

Behaviour Entering the Scales, the Crush and the Bail

The same description of behaviour was used to score animals during entry to the scales and the crush. The fact that mean scores for both were low indicates that the animal submitted easily to these movements. It may seem surprising that the scores were neither related to each other nor to temperament scores. However, it was observed that docile animals sometimes scored high or low for entry to the scales or the crush as did animals with temperaments classed as nervous, wild or aggressive. This suggests that slow or fast movement of cattle in yards may be obtained although the reasons for movement may be different. The docile animal may linger or move forward confidently whereas the nervous, wild or aggressive animal may hesitate or rush.

As the movement of the animal's head into a bail is not as simple as walking through a gateway, more detailed descriptions of behaviour were used to define scores for entering the bail than for entering the scales or the crush. However, the scores for entering the bail were intended to correspond with similar scores for the scales and the crush. The higher scores for entering the bail than for entering the scales or the crush, indicate that the animals either found this movement into the bail more difficult to perform and/or that it represented an experience which they were less willing to perform than entering the scales or the crush. The behaviour score for entering the bail gave no indication of an animal's temperament. The situation is probably similar to that when an animal is faced with a gateway, for example, when entering the scales or the crush. An animal may wait to go forward either because its temperament is good or because its bad.

The significantly high Hereford scores for entering the crush, compared with the low Angus and Shorthorn scores represented differences between these breeds. The large horns of the Hereford steers may have contributed to this, because the spread of their horns was often wider than the gateway into the crush (width 28 in.). However, this was only partly the reason because the differences between mean scores for horned and dehorned animals were not significant.

Breed differences for behaviour entering the bail were in the same directions as those for entering the crush but in this case Hereford scores were only significantly higher than Shorthorn scores. The observations on behaviour entering the scales, the crush and the bail, suggest that the Hereford cattle were more difficult to handle than the other breeds during movements through the yards.

Temperament

The effectiveness of the temperament scores allotted depends on the extent to which cattle showed variation in behaviour whilst under observation, on the extent to which details of behaviour were recorded and the objectivity used in this recording. The times spent in the bail during coat sampling and during skeletal measuring appeared to be long enough to get adequate variations in behaviour. The behaviour recorded was restricted to details which could be observed easily and described simply—it appeared undesirable to record impressions of emotions. To avoid any unintentional linking of behaviour scores with certain types of animals, for example, poor temperament with the unthrifty animals and good temperament with the thrifty ones, behaviour patterns were not translated into temperament scores until the series of observations on behaviour had been completed.

The descriptions of the temperament scores do not include all observations recorded, because some incidents occurred too rarely to be regarded as normal. However, when there was any doubt as to which behaviour score should

have been allotted to an animal, the highest of the likely scores was chosen.

In the breeds described in this experiment, Hereford and Angus cattle had significantly lower temperament scores than Shorthorns. The mean scores suggest that of the three breeds Herefords were the most docile and Shorthorns the least.

The general impression gained when handling these cattle was that Herefords were docile, Angus were restless or nervous and Shorthorns were unpredictable. The standard errors for temperament scores showed in Table V support this point of view. Although the differences between mean scores for sexes was not significant, it appears that steers had better temperament than heifers.

These observations were made over a period of 12 months and mean temperament scores did not show a downward trend during this period. In fact they fluctuated between 1·3 and 3·8. The reason for this is not clear although it may have been a reflection of the way the stockmen handled the herds when they were mustered for yarding and of the patience shown by observers and others when the animals were being handled in the yards.

Temperament for an individual cannot be effectively scored by observations on one occasion, because day to day variations in behaviour may be large. In this paper observations on steers were made on five or six occasions and three times on heifers. Three occasions are probably enough to get an estimate of group performance, but for individual scores it is suggested that behaviour be recorded on not less than five occasions.

The relation between temperament and live weight indicates that animals which are generally docile grow better than animals which are restless, nervous, wild or aggressive. Docile animals are desirable not only in relation to growth rate, but because they make the stockman's job a more pleasant one. It is claimed by cattlemen that cattle which are difficult to handle require more skilled management and facilities not normally required when handling cattle which are easy to handle. From the evidence presented in this paper on the absence of a relation between temperament and cattle movements entering the scales, the crush and the bail, cattle which are difficult to handle need not have bad temperament. These implications are important for registered breeders as it is likely that selection based on live weight gain may simultaneously lead to an improvement in temperament. On the other hand, selection based on ease of handling in yards may make the herd easier to handle but it will not necessarily improve herd temperament.

Summary

The observations reported in this paper concern the behaviour of 72 cattle, representing 12 steers and 12 heifers of each of the Hereford, Angus and Shorthorn breeds.

Behaviour was recorded as the cattle moved through yards at the following points—entering the scales, entering the crush, entering the bail and in the bail.

Behaviour when entering the scales, or the crush, or the bail was summarised by allotting scores within the range 1 (best) to 4 (worst). Behaviour in the bail was used to allot temperament scores within the range 1 (docile) to 6 (aggressive). The behaviour associated with each of these scores is described.

Scores allotted for entering the scales, the crush and the bail were neither related to each other nor to temperament, although mean scores for entering the bail were significantly higher than scores for entering the scales or the crush.

Differences between breeds were not significant for behaviour entering the scales. Hereford scores for entering the crush were significantly higher (worse) than scores for Angus and Shorthorns, but difference between Angus and Shorthorn scores were not significant. Breed differences for entering the bail were in the same direction as those for entering the crush, but in this case Hereford were only significantly higher (worse) than Shorthorns. Differences between sexes or between horned and hornless animals were not significant for any of these scores.

Herefords and Angus had lower (better) temperament scores than Shorthorns. Differences between sexes were not significant.

When the mean temperament score for each animal was compared with its live weight, animals with high temperament scores (greater than 2) had significantly lower body weights than those with low temperament scores (2 or less).

The difference between these behaviour scores and their implications so far as management practice is concerned, are discussed.

Acknowledgment

The author wishes to thank the Reserve Bank of Australia (Rural Credits Development Fund) for financial assistance, the Melbourne and Metropolitan Board of Works for permission to

use their cattle and their facilities, and particularly their staff for assistance with this work.

REFERENCES

Brownlee, A. (1950). Studies in the behaviour of domestic cattle in Britain. *Bull. anim. Behav.*, **8.**

Brownlee, A. (1954). Play in domestic cattle in Britain: An analysis of its nature. *Brit. vet. J.*, **110** (2), 48-68.

Brownlee, A. (1957). Higher nervous activity in domestic cattle. *Brit. vet. J.*, **113** (10), 407-416.

Fraser, A. (1957a). The state of fight or flight in the bull. *Brit. J. anim. Behav.*, **5,** 48-49.

Fraser, A. (1957b). The disposition of the bull. *Brit. J. anim. Behav.*, **5,** 110-115.

Kelley, R. B. (1943). Zebu-cross cattle in Northern Australia. An ecological experiment. *C.S.I.R. Aust. Bull.*, **172.**

Parez, M. (1933). Contribution a l'étude de l'insémination artificielle. Phychologie du taureau. Conservation de la semence à trés basse température (Thése Véter (Etat). Paris).

Schloeth, R. (1956). Quelques moyens d'intercommunication des taureaux de Camargue. *Terre et vie*, **2,** 83-93.

Scott, H. (1958). Inhibition of milk secretion as a function of temperament in cattle. *Aust. N.Z. Assoc. Advance Sci.*, Adelaide.

Tulloh, N. M. (1960). Behaviour of cattle in yards. I. Weighing order and behaviour before entering scales. *Anim. Behav.* (in press).

Accepted for publication **29th September, 1960.**

A NOTE ON THE EFFECTS OF GYMNEMIC ACID ON TASTE PERCEPTION

By M. R. C. LOVELL, C. G. GROSS* and L. WEISKRANTZ
Psychological Laboratory, University of Cambridge

It is a vexed question to what extent an animal tastes with its mouth, and how far it may be said to taste with its stomach. For instance, when it is demonstrated (Hughes, 1957; Sheffield *et al.*, 1954) that a non-nutritive substance, such as saccharin, will not only be preferred to water by rats, but will serve as an effective reward in a learning situation, one is led to the hypothesis that information from the taste buds alone can have a controlling influence on behaviour. (Saccharin passes through the mammalian body with its chemical form unchanged). On the other hand, Miller & Kessen (1952) have shown that rats can learn a T-maze for a milk reward delivered by gastric fistula. These results suggest that gastric events can signal the presence of a rewarding substance.

Clearly, there would be an advantage, when studying the relative importance of oral and gastric factors, in being able to eliminate oral factors without recourse to surgical interference with the oesophagus. And even in the oesophageal fistula preparation, there is a possibility that oral events could be influenced indirectly after absorption of various substances into the blood stream. Food selection following denervation of the oral region has been studied (Pfaffmann, 1952) but the surgery is difficult and the side effects may be extensive. For the same reason, cocaine injection has been found unsatisfactory (Weiskrantz & Gross, unpublished observations). This paper reports an attempt to exploit an interesting property of gymnemic acid and its effects on food selection.

The leaves of *Gymnema sylvestre* (an Indian plant) and a substance that can be purified from it, gymnemic acid, have been described by Power & Tutin (1904). The main effect of the substance, after it has been swilled around in the mouth for a minute or so, is to raise very considerably the threshold for the detection of sweet substances. The effect has been investigated by Shore (1892), Mhaskar & Caius (1930) and more recently by Warren & Pfaffmann (1959). Shore showed that an aqueous decoction of *Gymnema sylvestre* gives an effect that is no different from that of using weak solutions of the sodium salt of the derived gymnemic acid. The latter is expensive to prepare, and sufficient quantities for experiments are obtained much more easily by decoction.

The experiment to be described tested the effects of drinking a gymnemic decoction (GD) on choices by rats between a saccharine solution and distilled water, and between a sucrose solution and distilled water.

Apparatus

Twelve testing compartments for rats were prepared; each compartment had three wooden walls, and one metal wall. Bottle holders were fitted along the latter, two to a compartment. Once inside a compartment, no rat had any glimpse of any other rat. Glass bottles were used, fitted with rubber stoppers and curved metal feeding tubes. Each was checked for drip rate, which was found to be close to 1 ml. per hour.

A 0·0167 per cent. solution of sodium saccharin and a 6·4 per cent. solution of sucrose were used. These were found to be roughly equal in sweetness to the human tongue, and they differ only slightly from one of the sets of equal strengths given by Lemberger (1908). A decoction of *Gymnema sylvestre* was prepared by putting about 70 g. of gymnema leaves in a saucepan with just enough water to cover. This was brought quickly up to the boil then allowed to remain hot without actually boiling for about 15 minutes. The liquid was then strained off, cooled, and distributed neat to the bottles. A fresh quantity was prepared on each occasion just before a testing session.

Subjects

Twelve experimentally naive young male albino rats were used. These were divided into two groups of six. Both groups shared a large communal cage during non-testing periods.

Procedure (See Fig. 1).

The rats were adapted to a 23-hour hunger regime for several days. Then, (Condition A), Group 1 were given a choice for one hour per

*U.S. Public Health Service pre-doctoral fellow.

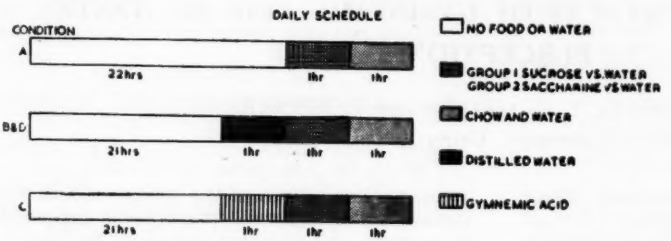


Fig. 1. Daily schedule for groups kept under listed conditions.

day (before the feeding hour) between the sucrose solution and distilled water, in the special compartments described above. Group 2 had a choice between the saccharine solution and distilled water. Neither group had access to food during this period. Appropriate randomization controls of bottle and solution position were made.

The first intention was to continue this condition until a criterion of three days' clear preference for the sweet substance was shown by both groups. This proved more difficult than previous work had suggested (Hausmann, 1933; Beebe-Carter *et al.*, 1948). To save time, Condition B was begun ten days after, when both groups were quite close to criterion.

In Condition B both groups were given one hour's access to distilled water before their choice situation. The positions of the bottles containing this distilled water were randomized. As in Condition A, both groups had access to food and water in the communal cage after the testing period.

Condition C was designed to test the effect of access to GD before the testing period on preference for sucrose and saccharin. After 21 hours' food and water deprivation, both groups were given access to GD in the compartments (the positions of the GD bottles were also randomized); this was followed by one hour's choice between a sweet substance and distilled water, and then one hour's provision of food and water ad lib. in the communcal cage.

Condition D was a repetition of Condition B.

Conditions B, C, and D lasted 3, 4, and 4 days respectively.

Results

As has been mentioned above, it was difficult to reach the desired criterion in Condition A. In Condition B, (after distilled water), however, it was reached immediately (Fig. 2). The probability of all six rats in a group preferring one particular substance to another by chance is equal to 0·016. Group 1 continued to show consistent preference to sucrose as against distilled water in Condition C (after GD), but Group 2 no longer preferred saccharin to distilled water to a significant degree. In Condition D (after distilled water), Group 1 continued as before; Group 2's saccharin preference was gradually reinstated —on the first post-GD day there was only a slight preference for saccharin. From the second day on, there was a clear preference for saccharin.

Discussion

Normally, saccharin preference is long-enduring (Sheffield *et al.*, 1954). One cannot explain the loss of saccharin preference in Condition C by suggesting that GD produced an aversion for liquids in general, because the *total*

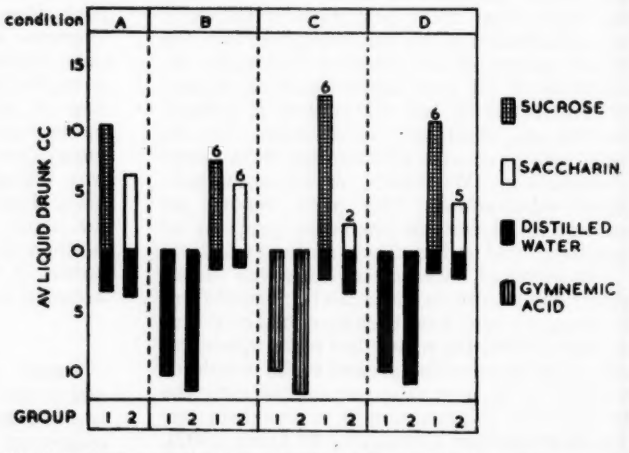


Fig. 2. Preference results. In two-bottle choice conditions, average amount consumed of each solution is shown in an upper and a lower portion of the bar graphs. Other bar graphs (unidirectional) show the amount of liquid consumed prior to the two-bottle choice situations, as indicated in the test and Fig. 1. Numbers over bar graphs in Conditions B, C, and D indicate the number of rats in each group of six who preferred the indicated solution to distilled water.

liquid intake of Group 2 in Condition C was not appreciably less than in Condition B. The results of Condition B, moreover, show that it is not just a case of *any* liquid removing saccharin preference. However, it has not been disproved in strict logic that liquids of the same tonicity as the gymnemic decoction might not have the effect claimed. Future research must obviously be directed towards controlling the tonicity variable.

It has been shown that, given the strength of the decoction and the concentration of the saccharin used, GD will eliminate preference for the latter. In view of the attempted equation of the strengths of the two sweet substances, the most obvious hypothesis for the continued preference of sucrose following GD is that it could be sustained by feedback signals from the stomach. There are, it is true, obvious methodological difficulties in equating the sweetness of saccharin and sucrose for the rat (rather than the human). Presenting the rat with a choice between saccharin and sucrose is not adequate since Miller's work has shown that gastric injection of sucrose will be reinforcing while saccharin will not be. (A preliminary study of rats' preference for the saccharin vs. sucrose was, in fact, carried out, the concentration being the same as used in the present experiment. No preference was immediately exhibited, although gradually sucrose came to be preferred). The oesophageal fistula preparation would seem to be necessary for making such an equation. Indeed, a rather major research project is suggested in comparing the thresholds for sucrose and saccharin when dependent upon taste alone (oesophageal fistula) or on gastric feedback alone (gastric fistula or GD) and in the normal preparation.

Gymnemic acid might be of vaulable assistance in the analysis of hypothalamic hyperphagia. Teitelbaum (1955) has presented evidence of heightened sensitivity to sensory qualities of their food by such animals. He comments that "sensory denervation studies should be crucial in clarifying the relative contributions of the internal environment and sensory qualities of the diet". Denervation, however, involves complicated side-effects as mentioned above; it might be possible to achieve Teitelbaum's aim more simply and satisfactorily with the use of gymnemic acid.

One interesting point is that sucrose ingestion by Group 1 went up markedly in Condition C. Mhaskar & Caius (1930) found that blood sugar level of their animals tended to drop after a gymnemic acid decoction had been put directly into their stomachs by fistula. It may be, then, that once sucrose was discovered by the rats, more was consumed in restoring the blood sugar balance to normal.

Summary

An investigation is presented on the effects of gymnemic acid—a substance known to raise the threshold for the taste of sweetness in humans—on saccharin vs. water and sucrose vs. water preferences in rats. Gymnemic acid eliminated the preference of saccharin over water, but failed to do so in the case of sucrose over water. The implications of the results are discussed, and further work is suggested towards analysing the relative effects of oral and gastric factors on preference. It is also suggested that gymnemic acid might prove a useful tool in the investigation of hyperphagia.

REFERENCES

Beebe-Center, J. G., Black, P., Hoffman, A. C. & Wade, M. (1948). Relative per diem consumption as a measure of preference in the rat. *J. comp. physiol. Psychol.*, **41**, 239-251.

Hausmann, M. F. (1932). The behaviour of albino rats in choosing food. II. Differentiation between sugar and saccharine. *J. comp. Psychol.*, **15**, 419-428.

Hughes, L. H. (1957). Saccharine reinforcement in a T maze. *J. comp. physiol. Psychol.*, **50**, 431-435.

Lemberger, F. (1908). Psychophysiche Untersuchungen über den Geschmack von Zucker und Saccharin. *Arch. ges. Physiol.*, **123**, 293-311.

Mhaskar, K. S. & Caius, J. F. (1930). A study of Indian medicinal plants. II. *Gymnema sylvestre*, Br. *Ind. med. Res. Mem.*, No. **16**, 1-49.

Miller, N. E. & Kessen, M. L. (1952). Reward effects of food via stomach fistula compared with those of food via mouth. *J. comp. physiol. Psychol.*, **45**, 555-564.

Pfaffmann, C. (1952). Taste preference and aversion following lingual denervation. *J. comp. physiol. Psychol.*, **45**, 393-400.

Power, F. B. & Tutin, F. (1904). Chemical examination of Gymnema leaves. *Pharm. J.*, **73**, 234-239.

Sheffield, F. D., Roby, T. B. & Campbell, B. A. (1954). Drive reduction versus consummatory behaviour as determinants of reinforcement. *J. comp. physiol. Psychol.*, **50**, 65-69.

Shore, L. E. (1892). A contribution to our knowledge of taste sensations. *J. Physiol.*, **13**, 191-217.

Teitelbaum, P. (1955). Sensory control of hypothalamic hyperphagia. *J. comp. physiol. Psychol.*, **48**, 156-163.

Warren, R. M. & Pfaffmann, C. (1959). Suppression of sweet sensitivity by potassium gymnemate. *J. appl. Physiol.*, **14**, 40-42.

Accepted for publication 9th March, 1960.

EFFECT OF LEARNING TO BE SUBMISSIVE ON STATUS IN THE PECK ORDER OF DOMESTIC FOWL

By STANLEY C. RATNER

Department of Psychology, Michigan State University, East Lansing

A number of the variables which are related to dominance-submissive relationships among domestic fowl are summarized by Wood-Gush (1955) and Guhl (1953). As they have noted, the variable of past fighting experience has received some experimental attention. Collias (1943), studying predictors of success and failure in encounters between pairs of birds, found that a bird's prior success or failure was one predictor of its subsequent success or failure. More recently Douglis (1948) reported observations of hens which lived part-time in a number of different groups. From these studies she concluded, "The role of conditioning (in terms of learning to dominate or submit) in these experiments is difficult to ascertain". (p. 176). She based this conclusion on the finding that some birds consistently held similar ranks from group to group but others held widely different ranks. A study which was explicitly designed to investigate the role of prior conditioning experience on ranks of domestic fowl, was conducted by Smith & Hale (1959). They found that a bird's rank in a small group could be radically modified as a result of avoidance conditioning experiences in which one bird became the conditioned stimulus for avoidance reactions of others in the group.

While these studies suggest the importance of prior dominating or submitting experiences on peck order relationships, they do not provide a clear answer to the question of the effects of a bird's prior experiences with an opponent on its rank in a peck order which does not involve that opponent. The present study was designed to investigate this question. The study was designed with each experimental bird serving as its own control. That is, the rank of the bird in the peck order was determined and then redetermined after encounters with a despot. This design was adopted in view of the stability of peck orders which is found to occur with mature domestic fowl (Guhl, 1953).

Materials and Methods

Four groups of mature White Leghorn chickens were used. Each group contained 14 birds which were maintained in indoor pens at the poultry laboratory of Michigan State University. The pens which housed each group were $8 \times 9 \times 14$ feet. Each had dirt and sawdust floors and an automatic feeder which extended the length of the pen. Pens were also provided with raised roosts, nesting boxes, water and grit. The pens were situated in a larger building which contained many other such pens.

The encounters between each experimental bird and the despot took place in a wire cage $24 \times 24 \times 27$ inches, which was located in a storage room across a hall from the living pens. A wire cage, similar to the one in which the encounters took place, served as a holding cage for the experimental birds during brief rest periods between encounters.

The study can be considered to have involved three phases: (*a*) determination of the original peck order, (*b*) encounters between experimental birds and the despot, (*c*) redetermination of the peck order. The three phases were then repeated with the same groups using different experimental birds.

The original peck order was determined in each of the four groups based on notations of fights, pecks, threats, and avoidance responses recorded during twenty 15-minute observations of each pen. A total of 1083 encounters were noted. The data were collected between March 1st and April 15th. Criteria used for defining the responses were the same as those used in a previous study (Ratner & Denburg, 1959). At the conclusion of the twenty observations, the peck order was determined for each pen. The rank of a bird in the peck order was evaluated according to criteria which are described in detail by Allee & Foreman (1955). Linear peck orders were assumed in assigning the ranks of the birds.

Following the determination of the original peck order, one experimental bird was selected from each pen for a series of ten encounters with a despotic hen which had been selected from another group. The experimental birds were selected from intermediate positions in the original peck orders so that either increases or decreases in ranks could occur. The original

ranks of the first set of four experimental birds were: 8th, 7th, 5th and 3rd. Each of these birds was placed in the cage with the despot for two 5-minute sessions every other day for five days. The despot was in the cage prior to the entry of the experimental bird and food was scattered on the floor of the cage. After placing the experimental bird in the cage, the experimenter noted the behaviours of the two birds during the two 5-minute encounters and removed the experimental bird to the holding cage for a 2-minute rest between the two daily encounters. The order of placing the experimental birds with the despot was varied from day to day.

During the 10-day period when the encounters were taking place, the peck order was redetermined for each pen to evaluate the effects of the encounters on the status of the experimental birds. Ten 15-minute observations were made at each pen for the redetermination of the peck order. The smaller number of observations was used because the original observations provided sufficient data to know the general structure of the order in each pen.

The four groups were allowed to rest for a week to insure the stability of the peck orders and then one more experimental bird was selected from each of the four pens. The ranks of these birds were: 1st, 4th, 3rd and 4th. These birds were selected to provide evidence about the effects of the encounters on higher ranking members of the peck orders. Each of the experimental birds was treated was described for the first set. Each had ten 5-minute encounters with the despot which had previously been used and the peck orders of the four pens were redetermined during the 10-day period when the encounters took place.

Following the main investigation, the despot and several of the experimental birds were given Triflorperazine, a commercial tranquilizer, to determine if the intensity of the encounters would be affected by this activity-reducing drug (Ratner & Ringer, 1959). The drug was administered orally with a pipette. The mixture was prepared with 50 mg. of drug per 1 c.c. of water, and this was given at the dose level of 1 c.c. of mixture per 1,000 g. of body weight. Dose level was based on work by Ringer (in press). Encounters between the treated birds took place 2 to 2½ hours after the mixture was administered.

Results

The main results of the effects of encounters with the despot are summarized in Table I, which shows the original ranks, new ranks, and changes in rank for each of the experimental birds. Data in the fourth column, which shows the change in rank of each experimental bird, indicates that the encounters with the despot led to a reduction in rank in the peck order for seven of the eight birds. The least reduction occurred for B4 (Pen 100) which moved from the top to the second place in the peck order. The greatest reduction occurred for B— (Pen 98) which moved from third to tenth place. The other experimental birds moved intermediate degrees. It will be noted that one bird, O, (Pen 96), rose in rank to the top position in the peck order from the third position. The changes principally involved a simple shifting in rank for the experimental birds in the pen. It was also observed that six of the seven birds, which were reduced in rank, pecked and threatened fewer birds than they had in the original determination of the peck order, and the seventh bird pecked and threatened the same number.

Table I. Original Rank, New Rank and Amount of Change in Rank in the Peck Order for Each Experimental Bird.

Bird and pen	Original Rank	New rank	*Change in Rank
R2 (100)	6	8	—2
Y2 (99)	7	9	—2
B2 (98)	5	8	—3
O (96)	3	1	+2
B4 (100)	1	2	—1
R1 (99)	4	7	—3
B—(98)	3	10	—7
R1 (96)	4	6	—2

*Reductions in rank in the peck order are indicated by— and increases by +.

Analyses of the behaviours during the encounters with the despot showed that the despot strongly dominated each of the experimental birds. That is, with the exception of the relationship between O, (Pen 96) and the despot, all experimental birds received at least ten pecks from the despot per day. During the remaining minutes of the encounter, the experimental birds remained immobile in submissive posture while the despot scratched and ate the food on the floor of the cage.

The two experimental birds, O (Pen 96) and B— (Pen 98), which showed unusual changes in

rank in the redeterminations of the peck orders, also had unusual relationships with the despot. Bird O (Pen 96), the bird which rose in the peck order, was the only experimental bird which was not completely submissive to the despot. Although it was pecked and threatened three or four times each session and it never pecked or threatened the despot, it did move about the cage and eat while the despot ate. Bird B— (Pen 98) showed the greatest reduction in rank. This bird received at least 20 pecks per 5-minute session and was judged to be the most severely treated. The treatment of the other experimental birds by the despot could not be quantitatively or qualitatively related to the changes in rank due to the limited variations in treatment and rank which were observed. The behaviour of the despot was quite stereotyped. The pattern of attacks, threats, and eating did not weaken during successive encounters with each bird.

Treatment with the tranquilizer Triflorperazine was undertaken to determine if the drug would alter the behaviour of the despot and/or submissive birds. The results of encounters between the despot and two experimental birds which were drugged, indicated that the aggressive and submissive behaviours were very similar to those observed during regular encounters. The despot pecked and threatened the drugged birds as frequently as it had previously. The visible effect of the drug was to give the birds a "sleepy appearance".

Results of encounters between previously used experimental birds and the drugged despot yielded findings similar to those above. The despot was sluggish in its responses but it pecked and threatened with great frequency and, in addition, quickly dominated two first-ranking birds with which it had had no prior experience.

Discussion

The results of encounters between experimental birds and a despot in a situation different from the home pen indicated that the experiences affected status in the peck order. Specifically, the encounters were associated with a reduction in rank in the peck order for seven of the eight birds and an increase in rank for one of the birds.

These findings can be interpreted in terms of the concept of conditioning of submissive reactions to the despot which generalized to the birds in the home pens. That is, the encounters can be considered as conditioning trials in which the movements of the despot (conditioned stimuli) were repeatedly associated with vigorous pecks (unconditioned stimuli) which led to submissive and avoiding responses (unconditioned responses), on the part of experimental birds. The finding that the experimental birds spent much of the time during encounters in submissive postures and avoiding the despot even when not being pecked supports this interpretation. The study by Smith & Hale (1959) reports that as few as ten presentations of electric shock (unconditioned stimulus) were required to condition a chicken to avoid another for two to nine weeks. The present study, while not using shock, involved many presentations of the unconditioned stimulus of pecking for each experimental bird. Generalization of a conditioned response to stimuli similar to the original conditioned stimulus is commonly found. Thus, the reductions in rank and in the peck orders involving the experimental birds are interpreted in terms of generalization of submissive reactions to birds in the home pens which approached or threatened the experimental birds.

This interpretation suggests that the experimental birds should have dropped to the bottom of their respective peck orders, which did not occur. That is, they continued to peck and dominate some birds in their pens. However, these birds had had long histories in their pens and there is no reason to think that conditioning of submissive and avoidance responses should obliterate previously learned aggressive responses. Also the very low ranking birds which did not "know what the experimenters had done to the experimental birds" continued to make their previously conditioned avoidance responses to the experimental birds. The birds which were instrumental in reducing the status of the experimental birds were principally those close to them in rank.

The extreme change in rank shown by the bird B—, which dropped seven places in the peck order, can be interpreted as a result of the extreme degree of conditioning of submissive and avoidance responses which occurred for it. The increase in rank shown by one bird (O) cannot be readily interpreted with the present concepts. The bird was dominated by the despot but was not pecked and beaten as the others were. One interpretation of the added vigour of the bird's responses in the home pen is in terms of the occurrence of conflict between fighting and submitting during the encounters which was resolved in the home pen into increased fighting.

The results of moderate doses of tranquilizer on the behaviour of the despot and other birds indicated that the drug did not alter the direction nor the degree of encounters between the pairs of birds.

Summary

The present study was designed to investigate the effects on rank in the peck order of encounters between experimental birds, which were taken from intact peck orders, and a despotic bird not involved in the peck orders. Four groups with 14 birds in a group were observed to determine the peck orders. A total of eight experimental birds was selected from these groups and each had a number of encounters with a despotic bird which was not a member of any of the groups. The peck orders were then redetermined to evaluate the effects of the encounters on the ranks of the experimental birds. Seven of the eight birds showed reductions in rank after the encounters, and the eighth showed an increase. The characteristics of the encounters were related to the changes in ranks of several of the experimental birds. Tranquilizers were found to have little effect on the behaviour of the despot or the experimental birds. The effects of the encounters are interpreted in terms of conditioning of submissive and avoidance responses which generalized to the home pens.

Acknowledgments

The research was facilitated by a grant from Michigan State University, and tranquilizer, known commercially as Stelazine, was supplied by Smith, Kline and French Laboratories. Mr. K. R. Miller assisted in the collection of data and Dr. R. K. Ringer advised on the dose levels of tranquilizer.

REFERENCES

Allee, W. C. & Foreman, D. (1955). Effect of an androgen on dominance and subordinance in six common breeds of *Gallus Gallus*. *Physiol. Zool.*, **28**, 89-115

Collias, N. E. (1943). Statistical analysis of factors which make for success in initial encounters between hens. *Amer. Nat.*, **77**, 519-538.

Douglis, M. B. (1948). Social factors influencing the hierarchies of small flocks of the domestic hen: Interactiors between resident and part-time members of organized flocks. *Physiol. Zool.*, **21**, 147-182.

Guhl, A. M. (1953). Social behaviour of the domestic fowl. *Tech. Bull.* **73**, *Agric. exp. Sta., Kansas State College*.

Ratner, S. C. & Denburg, M. L. (1959). The effects of age on the social organizations of chickens. *Quart. Bull. Mich. Agric. exp. Sta., Michigan State University*, **41**, 544-549.

Ratner, S. C. & Ringer, R. K. (1959). An activity cage and recorder for domestic fowl. *Anim. Behav.*, **7**, 245-247.

Ringer, R. K. (In press). Some physiological responses to tranquilizers. *Poult. Sci.*

Smith, W. & Hale, E. B. (1959). Modification of social rank in the domestic fowl. *J. comp. physiol. Psychol.*, **52**, 373-375.

Wood-Gush, D. G. M. (1955). The behaviour of the domestic chicken: A review of the literature. *Brit. J. anim. Behav.*, **3**, 81-110.

Accepted for publication 31*st August*, 1960.

DISPLACEMENT GROOMING IN THE CHAFFINCH

By C. H. FRASER ROWELL

Field Station for the Study of Animal Behaviour, Madingley, Department of Zoology, Cambridge

I. Introduction

The concept of the displacement activity, first formally stated by Tinbergen (1940) and Kortlandt (1940) drew attention to an apparent anomaly of behaviour. Most acts of behaviour occur in apparently directed sequences; not infrequently, however, short periods of behaviour occur when none of the animal's previous actions suggest an increase in the appropriate stimulation, and which serve no obvious purpose; for example, grooming occurs commonly in sexual and aggressive encounters in many birds (see, for example, Tinbergen, 1952). Both authors concluded that such activities were associated with conflict or thwarting situations, and Tinbergen (1940) described their main observervable characteristics as

1. occurrence "out of context", among functionally unrelated behaviour;
2. "irrelevance", i.e. absence of the external stimulation normally associated with the action;
3. incomplete or frantic performance.

It was originally suggested (Tinbergen, 1940, 1952) that this type of behaviour had neurological causal factors different from those producing the same behaviour in other circumstances. To stress this, Kortlandt (1940) proposed the terms "autochthonous" and "allochthonous" to distinguish the two types. In the first class the behaviour was "energized by its own drive", and in the second by the "drive built up by other activities" prevented from discharging in the conflict situation. This distinction was widely accepted. This apparently irrelevant behaviour, which was labelled "Ubersprungbewegung" or "displacement activity", is real and common, and the terms proved very useful in descriptive ethology. Both names imply a "surplus" hypothesis of motivation of displacement (van Iersel & Bol, 1958), and their widespread use among ethologists has often been taken to imply an equally widespread acceptance of this theory.

It has, however, become obvious in the last decade that this interpretation of displacement activity is in many ways unsatisfactory. First, the concept of drive and the hierarchical organization of nervous mechanism responsible for instinctive behaviour (e.g. Tinbergen, 1950), in terms of which the displacement activity was founded, have been increasingly criticized (e.g. Lehrman (1953), Kennedy (1954, 1958) and Hinde (1954, 1956). Second, of the characteristics of displacement activity listed above, the latter two are not necessarily present. Many displacement activities, and especially the commonest, feeding and grooming (Tinbergen, 1952), if not solely a response to direct stimulation, are at least strongly influenced by it (Armstrong, 1950), review, Moynihan (1955), Schmidt (1956), (Andrew, 1956 a and b), van Iersel & Bol (1958). Frequently, and especially in grooming birds, the movements are not incomplete or in any way different from the "normal" movements (e.g. Armstrong, 1950) review, van Iersel & Bol (1958), personal observation). Thorpe (1951) wrote "incompleteness or imperfect orientation. . . . is not a feature of displacement activity as such, but is merely a characteristic of all behaviour, resulting from low intensity drives. To summarize, it seemed that the "surplus" hypothesis was theoretically and neurologically improbable, that the characteristics of a displacement activity did not necessarily distinguish it from its normal occurrence, and that far from being "irrelevant", it was often at least influenced and possibly initiated by direct external stimulation. The sole remaining peculiarity was therefore the timing of the action, its occurrence out of context. Why did it occur so expressly in conflict situations, particularly when the two tendencies to perform incompatible actions were equally evident?

Andrew (1956b) suggested that peripheral stimuli inducive of grooming are continually present, but grooming is easily suppressed by other activities; for example, it is frequently interrupted or delayed by locomotion and other activities. When in conflict situations neither of the two primary conflicting tendencies can be expressed, grooming may occur in response to the usual stimulation. Similar suggestions were made by de Ruiter (Baggerman *et al.*, 1956). van Iersel & Bol (1958) made the first critical quantitative study of displacement, using grooming in breeding terms. They showed that grooming occurred when the two primary conflicting

tendencies were equal and opposite. They found no support for the "surplus" hypothesis, which they rejected, and they suggested essentially the same explanation as Andrew (1956b), that each primary conflicting tendency inhibited grooming, and that grooming was consequently disinhibited when the two primary tendencies were mutually inhibiting. Grooming itself they considered to be caused by the same "positive factors" as in any occurrnece of grooming, and they therefore rejected the terms "autochthonous" and "allochthonous". These positive factors were normally continually present at some intensity, but they differed from Andrew's explanation in that peripheral stimulation played only a small part. The observed variation in displacement grooming they attributed to variation in the degree of disinhibition.

The purpose of the present study was to investigate quantitatively displacement activity in a conflict situation which would be more strictly controlled and described than those used by previous authors. I have also tried to account for variation in grooming solely in terms ot variation of definable factors, especially peripheral stimulation, without postulating avoidable intervening variables, such as grooming drive.

II. Materials and Methods

1. The Chaffinch

Wild-caught male Chaffinches (*Fringilla coelebs*) were used. Many aspects of the behaviour of this species have previously been described by Marler (1952, 1955-56, 1956 a & b), Hinde (1953, 1955), and others.

2. Terms Used in Describing Grooming

Grooming implies all movements which contribute directly to the care of the body surface. In the Chaffinch it consists of preening, in which feathers of various parts are drawn through or nibbled with the bill; scratching with the foot; pecking at the feet or vent with the bill; feather settling, in which the body feathers are raised, and the body shaken (at high intensities, as after bathing, the latter component is greatly increased, when the behaviour is called "shaking"); and wiping the bill, normally on a perch, but sometimes on the ground. The last two movements are by far the most common, and this study deals largely with their occurrence. The individual grooming action, for example, bending forward, wiping the bill on the perch, and resuming an upright posture, I call a "grooming act"; a period in which one or more of these acts took place, limited either by locomotion or inactivity for more than 15 seconds, is called a "grooming bout". In conflict situations, the majority of bouts consist of only one act, and the two terms are synonomous. After bathing, however, most bouts contain many acts.

Throughout this paper, the term "peripheral stimulation" is used as a shorthand for stimulation affecting the body surface of the bird, in response to which the bird performs some sort of grooming behaviour.

3. Experimental Set-ups

Sexual and other social behaviour was avoided because of its seasonal nature and the difficulties of observing more than one animal simultaneously. "Thwarting" situations, which are in theory simpler than conflict situations, are probably academic abstractions, for attempts to produce them always result in some form of conflict (see also van Iersel & Bol, 1958). My experiments have all used approach-avoidance conflicts, in which the two conflicting tendencies can both be assessed by intention or completed locomotory movements. These conflicts were produced in two ways:

i. Hunger-fright conflict. Food is returned to a deprived bird, which moves towards it to feed. Before it feeds, it is frightened from the food by flashing an electric light bulb mounted in the food dish. In this way an approach-avoidance conflict can be maintained almost indefinitely.

ii. Owl mobbing. The mobbing of predators in general and owls in particular by Chaffinches and other passerines has been described by Hartley (1950), Hinde (1954), Marler (1956a), Rand (1941) and others. It is agreed that it is an approach-avoidance conflict, but the motives are uncertain. For my purposes this is irrelevant. I produced mobbing by placing a stuffed Little Owl (*Athene noctua*) a given distance from the bird's cage.

4. Recording Methods

The changing motivation of the bird is shown in oscillating movement. The bird's position, and other relevant behaviour, e.g. grooming, was continuously plotted on a strip of paper moving at 0·5 cm. per second. Both bird and plot were viewed simultaneously through an angled sheet of glass, acting as a half-silvered mirror; bird and pen point were kept superimposed, and the record thus made was accurate to $\pm$0·003 minute. (0·2 second). The paper used

was semi-transparent, and was analysed by laying over graph paper. In the following account, the word "significant" implies a probability of 0·05 or less, unless other figures are given.

III. Factors Controlling Grooming in Conflict Situations

A. Preliminary

The occurrence of grooming in any situation can be attributed to at least two sets of variables:

1. Peripheral stimulation, acting as a direct causal factor.

2. the occurrence of other types of behaviour which are incompatible with grooming.

It can be assumed that under certain conditions other internal factors, e.g. long- or short-term waning, would influence the response to stimulation. It has not been found necessary to consider this in the work described, presumably because grooming is too rare in conflict situations for these conditions to occur.

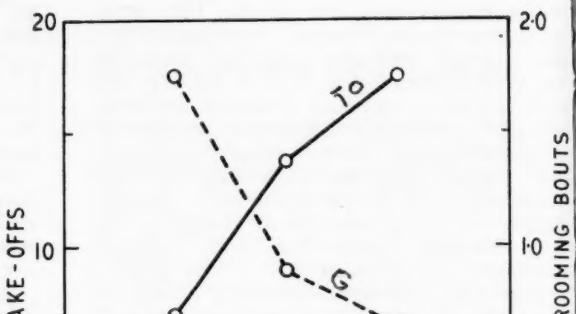


Fig. 1. Take-offs per minute (solid line) and grooming bouts per minute (broken line) in three situations: normal (N), hunger-fright conflict after 90 minutes deprivation (C), and hunger after 90 minutes deprivation (H).

When experimental conditions are kept constant, and a large number of trials is made and averaged, variation in grooming can be considered due to variation in these other activities. The most important of these is locomotion. The bird's behaviour may be divided into time spent moving, and time sitting still; only in the latter is grooming possible. Measures of locomotion and grooming would therefore be expected to vary inversely. This was shown to be correct in the experiment described below.

Chaffinches were observed in three experimental situations. These were:

1. Hunger, with a deprivation of 90 minutes.

2. Hunger-fright conflict, following a deprivation of 90 minutes.

3. Normal, in which the birds were not disturbed in any way.

Ten individual birds were used, and each bird was placed in each situation five times, according to a randomized pattern. Each trial was watched for thirty minutes, and the numbers of take-offs and grooming bouts were recorded. The results are expressed as average frequency per minute of observation time in Fig. 1. Despite the crudity of the measures used, there is a convincing inverse relationship between the two. A number of similar experiments were performed, and all gave the same result; unless one of the test situations increases peripheral stimulation by involving feeding, bathing, etc., grooming varies inversely with locomotion.

Now grooming is intermittent, in that not all pauses between periods of locomotion contain grooming bouts, even though peripheral stimulation appears to be at its maximum; for example, even in heavy rain grooming only occurs in less than 25 per cent. of all pauses.

Possible explanations for this, in terms of the factors already mentioned, are:

1. Variation in peripheral stimulation. This does not fit all cases; intermittent grooming is for example as characteristic of situations where variation is slight or absent as of others where it is probably greater.

2. Variation in length of pauses between locomotion. If the pause is very short, grooming cannot occur; thereafter, other things being equal, the probability of grooming occurring will increase with length of pause. This can be shown experimentally (Section C, p. 40).

If only these two factors were important, grooming would occur in all pauses over a certain length provided stimulation was adequate. This is not so; also, from 2 above, it seems that another factor is intermittently present. A lack of alternatives suggests that this is:

3. Variation in motivational state. In these conflicts the main motivational changes are between tendencies to approach and to advance. When the bird is stationary, these two tendencies must approach equality; however, they are not necessarily exactly equal, but may differ by an amount insufficient to correlate with a complete response. If the state when the two tendencies are exactly equal be called "equilibrium", then all pauses imply that equilibrium is being approached. However, in some causes, and always when the pause is associated with change of direction, equilibrium is at least momentarily attained.

This criterion of equilibrium, reached in some pauses and not others, would have the necessary characteristics of a third factor controlling grooming. It agrees with the older field descriptions of displacement activity as occurring "at the psychological moment", and also with the conclusions of Andrew (1956b) and van Iersel & Bol (1958), who considered that displacement grooming occurs when two primary conflicting actions, each of which singly was incompatible with grooming, are equally balanced. To summarize, I postulate that for a bird to groom in a conflict situation it must be:

a. subject to adequate external stimulation,

b. in a state of equilibrium with respect to the primary conflict,

c. in this state for long enough to respond to the stimulation by grooming; further, that variation in the observed grooming performance is referable to variation in one or more of these factors. The following three sections support this view.

B. Peripheral Stimulation.

1. *Introduction.*

It is common knowledge that grooming frequently follows an increase in peripheral stimulation; after bathing, feeding, drinking, or copulation, to mention only a few examples. It is therefore usually assumed that grooming is a response to peripheral stimulation, and if it is also granted that grooming is likely to decrease such stimulation, the explanation provides a feedback loop to co-ordinate activity with environment. The simplest view of grooming in conflict situations, where there is no apparent increase in peripheral stimulation, is therefore that here also grooming is a response of this sort. This explanation requires that there is a more or less continuous "background" level of input, with occasional peaks caused by additional stimulation, rather than sharp "ON" and "OFF" conditions. This agrees with the normal result of recording electrically from sensory systems in general.

The experiments described below show that variation in type and intensity of stimulation give the expected variation in type and frequency of grooming in both conflict and non-conflict situations, which is good evidence for the theory. The only serious objection to the view that grooming is a response to peripheral stimulation has been made by van Iersel & Bol (1958). They found regular sequential changes in grooming after bathing in terns, and concluded that this indicated a similar change in grooming drive following bathing. In the Appendix it is shown that the same type of grooming sequence occurs in Chaffinches, and also that this effect can be explained without this postulate. I therefore maintain the view that grooming is primarily a response to peripheral stimulation.

2. *Peripheral Stimulation Influencing Grooming in Conflict and other Situations.*

If grooming is primarily a response to peripheral stimulation changes in stimulation will produce changes in grooming, in both conflict and other situations. First, a general increase in stimulation should produce more grooming of all types, and second, an increase in one type of stimulation should produce a change in the composition of grooming. Both these effects are demonstrated in the experiments described below.

1. Conflict and normal situations in dry and wet weather. Chaffinches kept in individual outdoor aviaries 6 m. × 2 m. were observed for twenty minutes in both "normal" and "conflict" situations, and their grooming behaviour was recorded. The "normal" situation was undisturbed behaviour commencing immediately after a feeding bout; the grooming which normally follows feeding was included. The conflict situation was owl mobbing, produced by placing the stuffed owl on a shelf at one end of the aviary. All birds showed a typical approach-avoidance response.

The weather at the time of testing was also recorded, and the results were divided into three types on this basis;

(*a*) Wet (rain or heavy mist).

(*b*) Mild (dull, dry, still, air temperature above 40°F. (4·5°C.).

(*c*) Cold (dull, dry, still, air temperature 40°F. or below). Experiments which took place under

other conditions were discarded from the results. Between 20 and 30 readings were obtained for each condition.

The results show, firstly, no significant differences in the composition of grooming in the different weather conditions. Secondly, Table I shows the variation in frequency of grooming. Grooming does not differ between birds tested on "mild" days and on "cold" days. On "wet" days the birds groomed much more frequently than in the two "dry" conditions.

Table I. Frequency of Grooming in Different Weather Conditions. a., Normal Period Following Feeding, and b., in a Conflict Situation.

Weather conditions	No. birds tested	Average frequency of grooming (bouts per 20 min.)	
		Normal	Conflict
Wet	15	50·2	28·6
Mild	17	29·0	12·3
Cold	18	32·3	11·2

Differences between averages for Wet-Mild and Wet-Cold were significant in both conditions.

2. Conflict situations with and without (*a*) damp plumage, and (*b*) sticky bill.

The previous experiment showed that all types of grooming are more frequent when the body surfaces are wet. The next confirms this, and shows the effect of increased peripheral stimulation of a more limited area.

Birds were placed in a hunger-fright conflict situation after a deprivation of 75 minutes. After five minutes observation, during which grooming was recorded, either:

(*a*) the bird was sprayed with fine water droplets from a hand atomizer, or

(*b*) the bird was allowed to approach the dish and peck once or twice at the seed, but not to swallow an appreciable amount. The seed had previously been moistened with a strong sugar syrup, so that the bill was thus made very sticky.

After these procedures the behaviour was recorded for a further five minutes, and compared with that recorded before the increase in stimulation was applied. These tests were carried out on 4 individual birds, each tested between 8 and 12 times.

The results are shown in Table II. Both procedures resulted in a significant increase in total grooming. In the first one, where the body surface was generally affected, all types of grooming increased equally, but in the second one, where only the bill was dirtied, the increase is almost entirely bill wiping.

Table II. Grooming in Hunger-fright Conflict before and after (*a*) dirtying the bill, and (*b*) spraying with water.

	Grooming (acts/min.)	Percentage bill wiping	Takeoffs /min.	n.
a. Before dirtying bill	0·35	41%	8·0	10
After dirtying bill	0·54	56%	7·0	10
b. Before spraying	0·39	38%	7·7	8
After spraying	0·53	36%	8·1	8

n.=no. of trials made with different birds.

3. *Conflict Situations with and Without Continuously Wet Plumage.*

The methods used to wet the body surfaces in the two previous experiments were rather crude and imprecise, and the atomizer method further frightens the bird. I therefore arranged that a normal indoor cage could be completely filled with a continuous fine spray of water, remotely controlled from the hide by a tap. Grooming at two levels of peripheral stimulation could thus be more accurately measured.

A bird's behaviour was recorded for ten minutes in a hunger-fright conflict after 75 minutes deprivation. The spray was then turned on to a certain strength, and behaviour recorded for a further ten minutes. This routine was repeated 10 times on alternate days.

The results are given in Fig. 2. To interpret them it is necessary to anticipate the following section (p. 43). I show there that in approach-avoidance conflicts the frequency of grooming at any points correlates with the average length of visit to that point. These values are given in the figure, and it can be seen that in both conditions they are positively and significantly correlated. ($r.=+0{\cdot}91$, $P.<0{\cdot}03$). However, grooming is much more frequent in the "wet" condition; the total frequency of grooming bout is approximately eight times that in dry conditions, and from a calculation of the two regression equations to

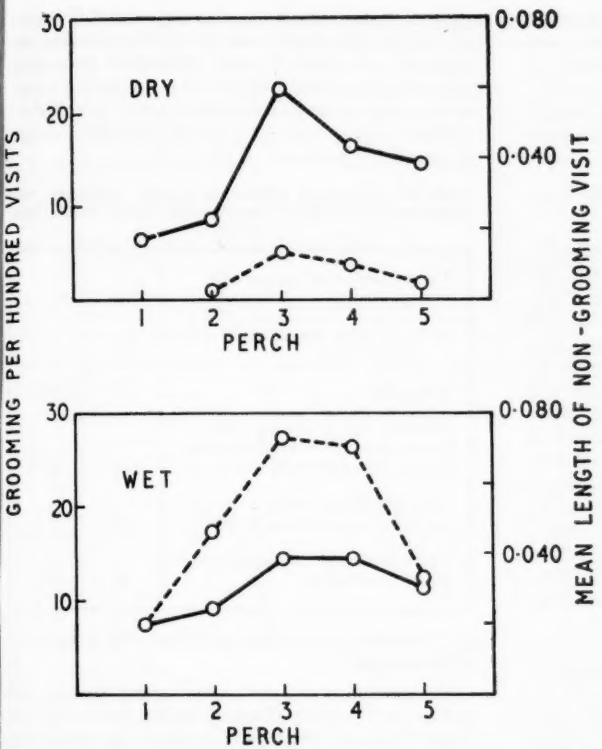


Fig. 2. Grooming per hundred visits (broken line) (y), and mean length of non-grooming visit (solid line) (x), at two levels of peripheral stimulation, DRY and WET. Constant hunger-fright conflict situation throughout.
Correlations: DRY r. = +0·91, P = 0·03, regression equation y = 111x—1·8
WET r. = +0·91, P = 0·03, regression equation y = 967x—11·4

give grooming in terms of length of visit, it is found that the appropriate value (m. in an equation of the form y=m. x+c) in "wet" conditions is 8·7 times that in "dry" conditions.

From these results I conclude that the composition and frequency of grooming in conflict and other situations is in the first place determined by the pattern and intensity of peripheral stimulation affecting the bird at that moment. However, this is not the only, nor necessarily the most important, factor affecting the occurrence of grooming at any particular time. It is reasonable to suppose that peripheral stimulation while varying in pattern and intensity, is continually present at some level, as is true of virtually any sensory modality. The observed differences in grooming in different experimental situations, in which the general level of peripheral stimulation can be considered constant, are due to other fact ors. These act by modifying the response to the primary stimulation, frequently suppressing it all together. These other factors are considered in the next two sections.

C. Available Time.

The next experiment shows the effect of variation in available time. Constancy in peripheral stimulation was simulated by averaging numbers of experiments performed in relatively constant conditions. To standardize the second variable equilibrium, the analysis described was restricted to pauses which involved change in direction (cf. p. 49).

The experimental situation was an owl-mobbing conflict. Individual birds were kept in cages 1 m. × 1 m. × 0·5 m. Each contained a food dish, a water dish, and a horizontal perch at slightly above mid height; this ran the length of the cage, and was divided into 6 equal zones painted alternately black and white. Forty-eight hours after the bird had been placed in the cage, a stuffed Little Owl was placed facing it, 3 m. from the end wall, at the same height as the horizontal perch (Fig. 3). This produced an approach-avoidance conflict, and the bird moved backwards and forwards along the perch, towards and away from the owl. Birds which appeared either too frightened or insufficiently frightened of the

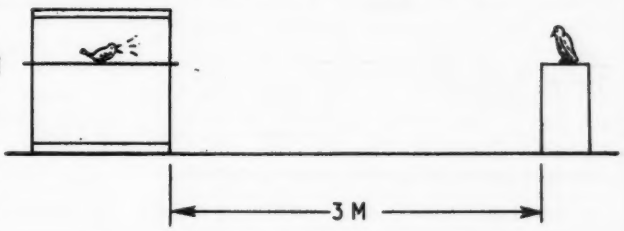


Fig. 3. The set-up used to produce owl mobbing conflict.

owl, and spent all their time at either of the cage walls, were discarded from the results, and only those retained which had an average position about the middle of the cage. Each trial was recorded from a hide for ten minutes; the results described were obtained from 29 trials with separate birds.

i. Comparison of Lengths of Grooming and Non-grooming Pauses.

When other factors are constant, the probability of grooming occurring will rise with the length of a pause. (p. 40). A first step to confirm this is to compare the length of pauses with and without grooming; by prediction, the latter should be shorter than the former. It may be objected that the average grooming pause will necessarily be longer than the average non-grooming pause by the length of time which it takes to groom. This is not a sound criticism because (*a*) grooming actions are frequently interrupted by movement; locomotion therefore does not have "to wait until grooming over", (*b*) the time taken to perform a grooming action is usually much shorter than the observed differences between grooming and non-grooming pauses (Tables III, VI).

Table III gives the mean and standard deviation of length of grooming pause and length of non-grooming pause in each of the six zones of the cages. The standard deviations of the non-grooming pauses were calculated from a sample of 1/20th of the whole population, obtained from the third 30 second period of each trial. The mean values obtained from individual measurement inside this sample agreed with the means obtained from the whole population by a method which did not involve individual measurement of each pause, and the sample was therefore accepted. It can be seen that the pauses without grooming are much the shorter; the differences are all highly significant ($P<0.01$). Similar results are obtained if each individual grooming pause is compared withthe non-grooming pause at the same zone which immediately preceded it; Table V shows that the grooming pause is longer in about 90 per cent. of all cases.

Table IV. Length of Grooming Pauses Compared with Immediately Preceding Non-grooming Pauses in the Same Zone.

Total number of pauses with grooming	356	
A comparable period could not be found in	134	
Remainder	222	100%
Of these, the grooming pause is longer than the immediately preceding non-grooming pause in	184	83%
The preceding pause is longer but is itself a grooming pause in	16	7%
The preceding non-grooming pause is longer in	22	10%

ii. Correlation of Length of Pause with Frequency of Grooming

As grooming occurs in the longer pause, and the average length of pause differs from zone to zone (i, above), one would expect most grooming to occur in zones which have on the average the longer pauses. There is here a danger of circular reasoning. I gave above (p. 44) my reason for believing that length of pause influences the occurrence of grooming, and not the reverse, but it is none the less important not to include grooming pauses when calculating the average length of pause. These, being considerably longer

Table III. Comparison of Lengths of Grooming and Non-grooming Visits to the Various Zones.

Zones:	Away from owl.					Towards owl
	1	2	3	4	5	6
Non-grooming pauses: — mean	0·020	0·037	0·043	0·030	0·031	0·026 min.
— s.d.	0·015	0·007	0·021	0·008	0·017	0·018
Grooming pauses (all types of grooming summed):						
— mean	0·085	0·073	0·093	0·089	0·103	0·073 min.
— s.d.	0·024	0·045	0·045	0·047	0·038	0·028

Table V. Frequency of Grooming in Each Zone in a Conflict Situation (owl mobbing).

	Zone: 1	2	3	4	5	6
a. Number of pauses with grooming	30	21	39	36	34	19
b. Total number of pauses	2548	575	563	838	767	731
c. Frequency of grooming per hundred visits	1·18	3·65	6·93	4·30	4·43	2·60
d. Average length of non-grooming pause (from Table IV)	0·020	0·037	0·043	0·030	0·031	0·026 minutes
e. Correlation between *c.* and *d.*: $r=+0{\cdot}90$, $P<0{\cdot}02$, regression equation (length of pause, y, in terms of frequency of grooming, x) $y=0{\cdot}0035x + 0{\cdot}017$ (min.)						

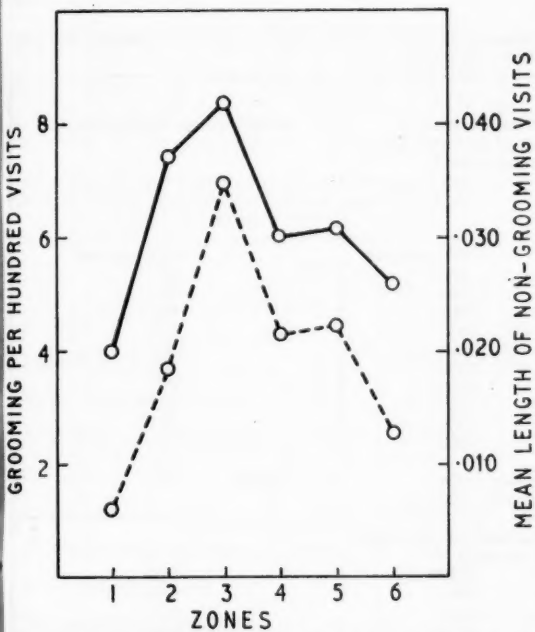


Fig. 4. Grooming per hundred visits (dotted line) and mean length of non-grooming visits in each zone of the cage during owl mobbing.

than the average, might superimpose a false correlation between the two values. To show indubitably the influence of length of pause on frequency of grooming, the latter must be shown to correlate with the average length of non-grooming pause.

Table VI gives the total number of pauses in each zone, and the number of grooming pauses in each zone. From this is derived the values for frequency of grooming per hundred pauses. The average length of non-grooming pauses was given in Table III, and is repeated in Table V. These two sets of values are plotted in Fig. 4. There is a good positive correlation; ($r = +0{\cdot}9$, $P < 0{\cdot}02$). Thus probability of grooming varies directly with average length of visit.*

iii. The Minimum Length of Grooming Pause.

In Table V the regression equation expressing probability of grooming in terms of length of visit is given. From this it can be seen that grooming can be expected to be nil (at the level of probability associated with these figures) in pauses of 0·017 minutes or less. Fig. 5 gives the actual distribution of grooming pauses of different lengths, showing a sharp cut-off at or just below 0·020 minutes.

iv. Length of the Grooming Motor Patterns.

Observations show that the grooming pause is normally much longer than the time spent in the action itself. From the previous section, one would suggest that the value of 0·017 minutes obtained would correspond to the length of the shortest grooming action. However, grooming actions frequently seemed much shorter than this (1 second = 0·016 minutes), so the actual lengths were measured by cine film. (Table VI). This showed that the average lengths of the commonest grooming actions are in fact considerably less than the minimum length of

*Tugendhat (1958), gives data which suggests a similar relationship between available time and comfort movements in the Three-spined Stickleback. She shows a straight line relationship between comfort movements and a measure which she considers proportional to the total length of time spent in the zone, the square of the number of 'advances'.

grooming pause recorded. However, associated with the grooming action is other, less easily defined behaviour, visible in the cine film, which goes to make up the whole act of grooming, as opposed to just sitting still. Some of these are mechanical preparations for the motor action, as when the bird shifts its weight across to one foot before lifting the other one to scratch itself; or as in bill wipin

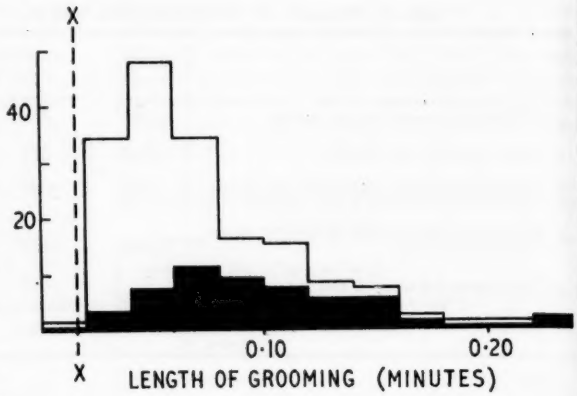


Fig. 5. Frequency distribution of grooming pauses of different lengths during owl-mobbing experiments. The blacked-in area represents feather settling, the rest bill wiping. The broken line X—X represents the calculated value at which the probability of grooming approaches nil. (0.017 min.).

Table VI. Analysis of Lengths of Different Types of Grooming, from Cine Film. (Mainly Chaffinch material, but some other finches included).

I Grooming bout	II Length of motor pattern (commencment of down-stroke to end of upstroke)	III Length of grooming period
a. Billwiping (No. of strokes/act in parenthesis)		
BW (1)	·003 minutes	·025 minutes
BW (1)	·004	·017
BW (1)	·004	·019
BW (1)	·005	·014
2 BW (1, 1)	·003, ·003	·016
3 BW (2, 1)	0·004, ·006, ·002	·025
2 BW (2, 1)	·010, ·006	·026
BW (2)	·005	·011
BW (1)	·007	·013
BW (2)	·006	·012
BW (2)	·008	·014
	Mean (single stroke) ·004 Mean (double stroke) ·007	Mean ·017
b. Feather settling	(raising of feathers to lowering of feathers)	
FS	·030*	·030*
FS	·007	·010
FS	·011	·019
FS	·016*	·016*
	Mean ·016	Mean ·019
c. Scratching.	(foot off ground)	
SK	·003	·019
SK	·014	·021
SK	·022	·030
	Mean ·013	Mean ·023

*The end of lowering the feathers could not be clearly defined in some of these cases, and motor pattern could not be separated from grooming period.

g (Marler, 1956b), when just before commencing the down stroke, the bird pauses and appears to fixate the branch stereoscopically with the temporal foveae. However, there is commonly a further "pre-grooming posture" preceding these actions. The salient characteristic of this is absolute immobility, lasting usually just a brief moment immediately before the grooming proper begins. In Table VI the average length of the "grooming period" is given for each type of grooming; this is measured from the assumption of this pre-grooming posture to the end of the motor action. The average of this measure corresponds well with the value of the minimum length of grooming period found experimentally.

v. Length of Pause Associated with Different Kinds of Grooming.

The data already given suggest that the length of grooming pause differs for the different kinds of grooming. Thus Fig. 5 shows different peak values of length of pauses with feather shuffling and pauses with bill wiping. Table VII shows the mean length and standard deviation of all pauses with (*a*) bill-wiping, (*b*) feather-settling, and (*c*) compound bouts (i.e. bouts including more than one kind of grooming). Only these types of grooming were common enough to be analysed in this way. The mean compound bout is significantly longer than mean feather shuffling, which is itself significantly longer than the mean bill wiping.

Table VII. Mean Lengths of a. visits; b. Pauses within Visits; c. Pre-grooming Part of Pause Associated with Bill Wiping and Feather Settling.

	Mean (minutes)	S.D.
a. *Visits.*		
Visits with bill wiping	0·087	0·079
Visits with feather settling	0·129	0·117
Visits with compound bouts	0·174	0·076
c. *Pauses*		
Pauses with bill wiping	0·059	0·033
Pauses with feather settling	0·098	0·048
c. *Pre-grooming pauses*		
Pre-grooming pauses followed by bill wiping	0·023	0·013
Pre-grooming pauses followed by feather settling	0·048	0·025

Where does this difference occur? Itis unfortnuately impossible to answer this accurately without filming a large number of examples, and the cost of this was prohibitive. On the ordinary record made on a moving paper strip, only three measures can be made for each grooming visit. These are (*a*) the total length of visit—that is, the length of the pause and also of the locomotion before and after the pause while entering and leaving the zone; (*b*) the length of pause; and (*c*) the length of pause before the actual motor pattern commenced. These values are shown in Table VIII for bill wiping and feather settling. These two actions differ significantly in all three measures, feather settling being the longer throughout.

From this table it can be seen that:

1. the average time spent in locomotion during a visit is the same (about 0·030 minutes) for both kinds of grooming. This value would not be expected to differ.

2. The average length of the period before the grooming act differs significantly. This suggests that the length of pre-grooming posture, described in the previous section, may be on the average longer in the case of feather shuffling.

3. This difference is not enough to account for the total difference in length between the two kinds of pause. The remainder, (0·012—0·015 minutes) presumably reflects the difference between the average lengths of the two motor patterns. This is the same order of difference as that found from the cine film (0·009—0·012 minutes), in spite of the fact that so few feather settlings were recorded on film (Table VI).

I conclude therefore that these types of grooming, and probably others too, take different lengths of time to perform. The actual motor patterns differ in length, and so also does the length of time before grooming commences, a period which seems to be functionally associated with grooming.

vi. Effect of Average Length of Pause on Average Composition of Grooming.

The different kinds of grooming have been shown to take different lengths of time. The three commonest kinds, in order of increasing duration, are bill wiping, feather shuffling, and compound bouts (Table VII). In ii above it was shown that grooming is influenced by the length of time available to it; that is, it is dependent upon the probability of interruption. Table III

gives the average length of non-grooming pause in each of the different zones; they are longest in the centre of the cage, and shortest at the two ends.

Now the types of grooming which take the longest to perform will be the most susceptible to interruption by a resumption of locomotion. If therefore the composition of grooming in each zone is examined, it would be expected that in the middle of the cage, where visits are longer, the long compound bouts would be most frequent, whereas at the ends of the cage, where visits are short, bill wiping would be the most numerous type of grooming. Table VIII shows that this is the case.

The possibility that the type of grooming determines the length of the pause, rather than the reverse, can be disposed of as follows:

(1) This cannot be reconciled with the correlation between frequency of grooming and average non-grooming visit (ii above).

(2) It provides no explanation of the marked difference in distribution of the different kinds of grooming.

vii. The Period of Response to Stimulation.

It is probable that peripheral stimulation is as frequent and intense during locomotion as in pauses, but response is impossible. Grooming is not more intense in pauses which follow long flight periods than after short ones, and it could therefore be argued that the grooming is primarily a response to stimulation perceived after locomotion has ceased. If so, one might expect to find a period of inactivity immediately prior to grooming, during which stimulation is perceived and responded to. This hypothetical period could be identified with the period of "pre-grooming posture".

One reason for the greater frequency of grooming when peripheral stimulation is increased could be that a shorter pre-grooming period of this sort suffices when stimulation is high. To investigate this I filmed thirty minutes of hunger-fright conflict in "DRY" and "WET" conditions (p. 42). Only bill wiping occurred often enough in both conditions for a comparison to be made, and this comparison is presented in Table IX.

1. The motor action is longer in "WET" conditions. This is due to the greater number of "wipes" per act; the difference is significant.

2. The length of the pre-grooming posture is smaller under the conditions of high stimulation, but the difference is not significant. The populations compared (8 and 14) are unfortunately too small to allow a final decision.

Another indication of the same trend can be derived from the results given in Fig. 2. If the regression equations for the length of pause in terms of frequency of grooming are calculated from those data, the results are:

"DRY" conditions; $x=0{\cdot}007y + 0{\cdot}019$ minutes.

"WET" conditions: $x=0{\cdot}0008y+0{\cdot}016$ minutes.

Thus the length of pause at which grooming can be expected to approach nil is shorter when stimulation is high, as would be expected by the hypothesis; once again, however, the differences are not significant.

Summary and Conclusions

These results show that grooming is profoundly affected by interruption caused by the resumption of locomotory activity. As the different kinds of grooming take different lengths of time, the probability of interruption influences

Table VIII. Effect of Mean Length of Visit on Composition of Grooming.

	Zones: Away from owl 1	2	3	4	5	Towards owl 6
Mean non-grooming pause	0·020	0·037	0·043	0·030	0·031	0·026 min.
Bill wiping as % of total grooming	66·6	52·4	56·4	50·0	58·8	89·5
Feather settling as % of total grooming	30·0	33·3	30·8	25·0	26·5	10·5
Compound bouts as % total grooming	3·3	14·3	12·8	19·4	8·8	0

Table IX. Comparison of Bill Wiping in Hunger-fright Conflict at Two Levels of Peripheral Stimulation, 'WET' and 'DRY' (ciné film analysis).

	'DRY' N=8	'WET' N=14
Length of grooming action	·005 ± ·002 min.	·010 ± ·003 min.
	P=0·002	
(mean no. of 'wipes' per action	1·1	2·6
Length of grooming action plus pre-grooming posture	·008 ± ·002	·013 ± ·003
	P = ·0001	
Length of pre-grooming posture	·003 ± ·001	·0022 ± ·0018
	P = 0·70	

not only the frequency of grooming, but also its composition. The composition of grooming has been used as a measure of "intensity of grooming drive" or of type of stimulation, but without allowing for this effect; conclusions reached in this way may need review. Not only can the grooming action itself be interrupted, but the existence of less obvious pre-grooming behaviour on many occasions implies that a grooming activity can be interrupted before the action itself has begun. Further, from the postulate of equilibrium (it follows that either the grooming motor pattern or the pre-grooming period could be interrupted by a departure from equilibrium, insufficient in itself to cause actual locomotion, or even perhaps intention movements of locomotion. The characteristic "incomplete, frantic or non-orientated performance" of displacement activities can also be attributed to interruption of the activity by a departure from the equilibrium state. The influence of the equilibrium state on grooming is demonstrated in the next section.

D. Equilibrium

The postulated conditions of equilibrium in a conflict situation, when the two opposite tendencies of the primary conflict are equal, cannot of course be directly observed. A mere absence of overt signs of either tendency is not adequate, as explained on p. 41. Consequently reliance must be placed on indirect evidence of when equilibrium is and is not present.

When a pause is accompanied by a change in direction, equilibrium has been reached, for here the tendency to advance has changed into one to retreat, or v.v., and at some stage they must have been equal. When a pause is not accompanied by change of direction, equilibrium may or may not have been reached. Often it seems that it has not, for intention movements in one direction persist throughout the pause. If equilibrium is a condition for grooming, grooming should be more frequent in pauses involving change of direction than those pauses which do not. The data obtained from the owl mobbing experiments described were analysed to this end.

The horizontal perch is divided into 6 zones (p. 43). The birds' larger movements can be divided between these zones. A visit to a zone may be of two sorts; the bird may enter it from the preceding zone, continue through it and into the next zone, without change in direction—a "through" visit; or it may enter from the preceding zone, change direction, and return to zone from which it came—a "turn". Table X shows the relative numbers of "through visits" and "turns" with and without grooming. This shows a very significant association between "turns" and grooming.

The same treatment of results obtained from hunger-fright conflicts gives the same results. Of 162 grooming bouts recorded during one experimental series of this kind, 149 (92 per cent.) were associated with change of direction. Tugendhat (1958) obtained very similar results, showing that 93 per cent. of "comfort movements" occurring in approach-avoidance conflicts in Three-spined Sticklebacks were associated with change of direction. From this (and other) evidence she concluded that comfort movements occurred when the two tendencies to approach and to avoid were equally strong; that is, at equilibrium. However, in the light of

Table X. Association of Visits with Grooming with Change of Direction.

	Turns	Through visits
Total number of visits	5983	12146
— as a percentage	28·1%	71·9%
Total no. of visits with grooming	179	39
— as a percentage	81·2%	17·9%
Mean length of non-grooming pause	0·028 ± 0·017	0·007 ± 0·005 min.
Mean length of grooming pause	0·088 ± 0·100	0·106 ± 0·180 min.

the previous section, proof of the association between equilibrium and grooming demands that the through visits were as long as the turn visits. This is not clear in Tugenhat's (1958) data, and is not the case in my own experiments, where through visits were on average less than half the length of turn visits. It is therefore necessary to compensate mathematically for the extra length of the turn visits. In the previous section (Table V), an equation was derived showing the relationship between probability of grooming and length of turn visit. Similar information about through visits cannot be obtained in this way, as no correlation between the two measures can be obtained. As an approximation, one must make the assumption that the relationship is the same in the two types of visits. Thus we have the relationship between length of visit and probability of grooming, and also histograms of frequency of visit against length of visit for both through and turn visits. From this information, the expected ratio of grooming in through and turn visits can be obtained.

The histogram of frequency of visits v. length of visit, together with the relation between probability of grooming and length of visit, can be used to derive a histogram of frequency of grooming v. length of visit. Thus for visits whose length lies between t and dt, the corresponding frequency of visit will be, say, N, and the probability of grooming P. Therefore the frequency of grooming will be NP. In this way, by multiplying the ordinates of the two curves at corresponding abcissae, the value of the corresponding co-ordinate of the histogram (frequency of grooming v. time of visit) is obtained. The total number of grooming acts in visits between t_1 and t_2 is given by the area under the histogram; in particular the ratio of number of grooming visits in both populations of visits (i.e. through and turn) will be the ratio of the areas of the histogram corresponding to the two populations. If this is done, a ratio (grooming through visits: grooming turn visits) of 1:1·2 is obtained, whereas the observed ratio (from Table X) is 1:4·6. This is significantly larger ($Chi^2=6·3$, $P=0·01$), and shows that the probability of grooming occurring in through visits is several times less than would be expected merely from their shorter length. On the basis of the preceding arguments I conclude that the extra factor favouring grooming in turn visits is the greater probability of equilibrium, and that this state is very much less common in through visits.

Van Iersel & Bol (1958) presented strong evidence of a different sort that grooming occurred in conflict situations when the two opposing tendencies approached equality. On these various grounds I accept the postulate that equilibrium is a factor controlling grooming in conflict situations.

IV. The Effect of Intensity of Conflict on Grooming Behaviour

The surplus hypothesis of displacement activity implied that increase in the intensity of conflict would cause an increase in the intensity or frequency of displacement. Van Iersel & Bol (1958) correlated displacement activity with a state of "effective equality"; in this state, they suggested, grooming took place as a response to the normal "positive factors", and they rejected the surplus hypothesis. However, they also recorded changes in grooming as intensity of conflict increased, of a type which agreed well with the forecasts of the surplus hypothesis. These were increases in *a.* the frequency of grooming, and *b.* the intensity of grooming.

To explain these they postulated changes in the quality of "effective equality". I will return to discuss these results and postulates in sections

4 and 5. below, but it is first necessary to show that in my own experiments on the effect of increasing conflict:

a. increase of deprivation in the hunger-fright conflict is equivalent to an increase in intensity of conflict;

b. the conclusions derived from the owl-mobbing conflict are equally applicable to the hunger-fright conflict.

1. Correlation of Intensity of Conflict with Degree of Deprivation.

The hunger-fright conflict situation relies (p. 00) on balancing the tendency to approach the food dish by a frightening stimulus. One would expect subjectively and also on the basis of comparable work on rats, that the tendency to approach the food dish would increase with increasing deprivation. If so, the intensity of the conflict as a whole will increase with deprivation. Observation of conflict situations of this sort after increasing deprivation supports this idea, as shown in the experiment described below.

Birds were kept in individual cages 2 m. × 1 m. × 1 m., which were furnished as shown in Fig. 6. After deprivations of 30, 75 and 120 minutes, the food dishes were replaced in the cages, thus producing approach-avoidance conflict. A total of 20 ten-minute trials were made with 5 birds in each condition. The to and fro motion of the bird took the form of flights between the transverse perches; a pause can therefore be defined according to the perch on which it took place. A full advance to the dish in order to feed would therefore go perch 1—perch 2—perch 3—perch 4—perch 5—fly to ground and walk towards dish—feeds, or frightened away by flash.

I call this walk between perch 5 and the dish an "approach". It gives a sixth measure of movement in addition to the five perches. At any point a bird may break off an advance and retreat. This is very frequent during approaches. An approach which continued without this right up to the dish and had to be stopped by flashing the light I call a "repulsed approach".

The behaviour shown in the different deprivations differs as described below.

1. Fig. 7 shows (*a*) the number of visits and (*b*) the amount of time spent at each of the 6 possible spatial positions, converted to a percentage of the total for all positions. This line is plotted for each deprivation. With increasing deprivation there is a steady increase for the values at the positions nearest the food dish, and a decrease in those farthest away. Thus the more deprived birds approach the food oftener, and spend more time near it.

2. The proportion of approaches which had to be repulsed increases significantly with deprivation.

Thus increasing deprivations increases the tendency to approach the food dish, and this is balanced by an increase in the absolute and relative number of frightening stimuli required to maintain the conflict. Therefore increasing deprivation represents increasing conflict intensity in these experiments.

2. Changes in Overall Frequency of Grooming with Increasing Intensity of Conflict.

Grooming behaviour was recorded during the experiment described above. The frequency of grooming (uncorrected totals) drops over the range of increasing conflict in all but one individual. The drop is sharpest in the range 30-75 minutes deprivation, and most birds show increase in the range 75-120 minutes deprivation. The results for individuals are shown in Fig. 8. The results are repeatable; Fig. 9 shows summed totals derived from 4 different birds, 16 trials in each situation, 1 year later.

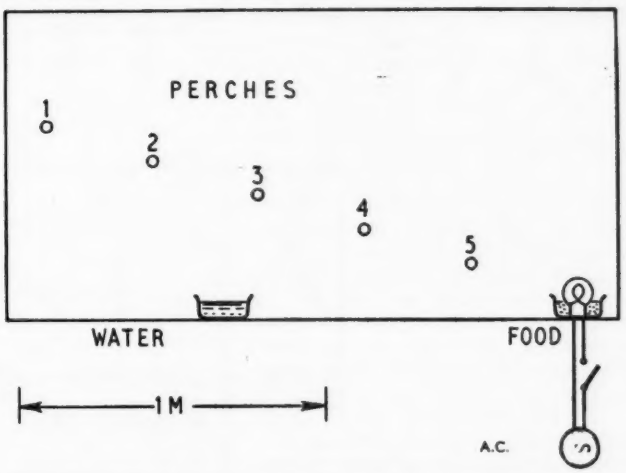


Fig. 6. Side elevation of the cages used in hunger-fright conflict experiments.

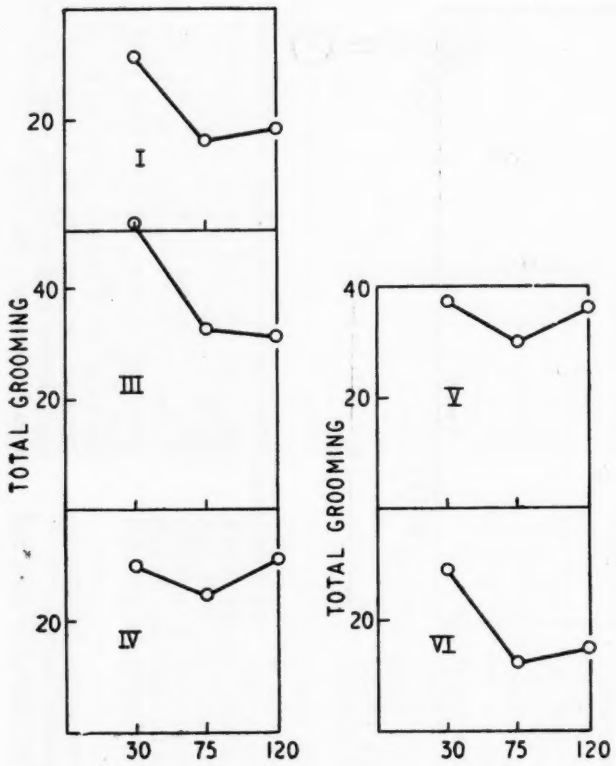


Fig. 8. Total grooming bouts recorded from 5 individual birds in identical hunger-fright conflict experiments.

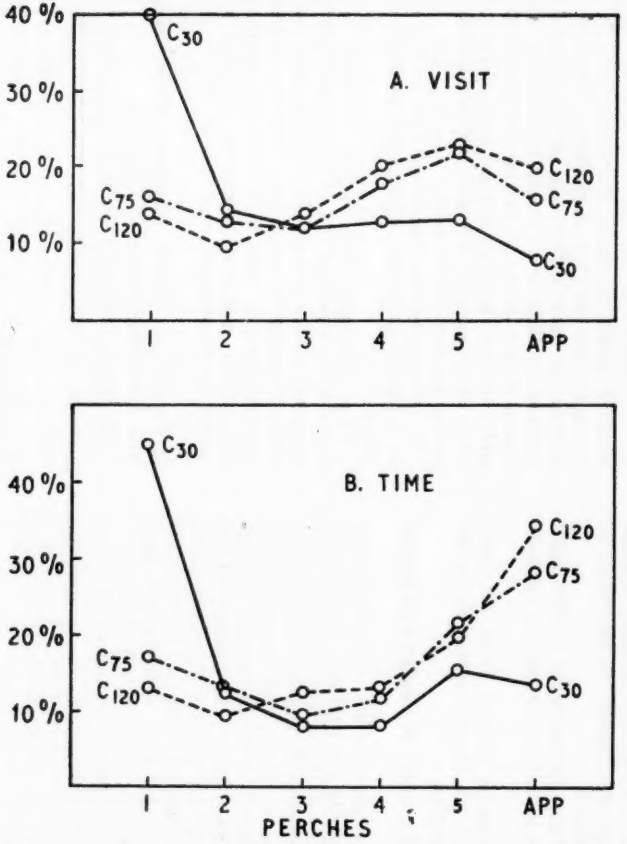


Fig. 7. A, number of visits, and B, total time, spent at each of the 6 possible spatial positions in the cage during hunger-fright conflict experiments. Separate plots are drawn for the different intensities of conflict, after 30 minutes (solid line), 75 minutes (broken line), and 120 minutes deprivations (dotted line). The value at each position is a percentage of the total of all six positions.

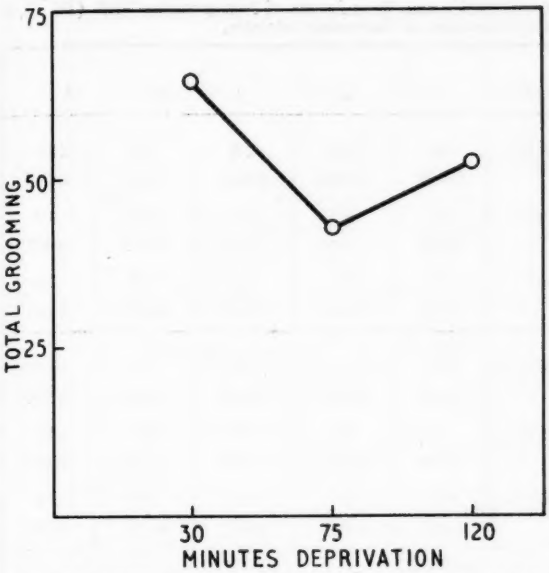


Fig. 9. Total grooming bouts recorded from four birds in further hunger-fright conflict experiments.

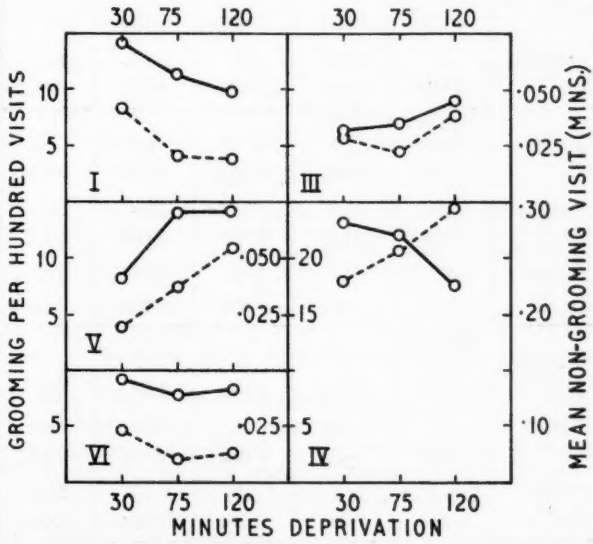


Fig. 10. Correlation between grooming (grooming bouts per hundred visits, broken line) and average length of non-grooming visit (solid line) in five birds in identical hunger-fright conflict experiments of different intensity.

If these values for total grooming by each individual in the three conflict intensities are corrected for the total number of pauses made on the perches, then it is seen that in 4 out of the 5 birds this value (grooming per hundred visits) correlates with the average length of visit. With the exception of this one bird (which is exceptional throughout the series), the frequency of grooming does not increase with deprivation; further the changes which do take place correlate with average length of pause, strongly suggesting that the main factor is change in the available time with increasing conflict, Fig. 10.

3. Correlation of Frequency ofGroom-ing and Average Length of Pause per Perch.

In the owl-mobbing conflict situ-ation (Section III), the frequency of grooming was dependent on the average length of time spent at each perch. Table XI gives the frequency of grooming, corrected for number of pauses, and the average length of non-grooming pauses, for each perch in the three conflict situations:*

Table XIa gives the average values obtained from all birds, and Fig. 11 the same graphically. In spite of the fact that one individual (Bird IV) does not show this correlation, the others do to such an extent ($r. + 0{\cdot}85 = + 0{\cdot}92$, $P<0{\cdot}05$) that these averages show positive significant correlations. The same measures for the individual birds are also given (Table XIb). Naturally, the figures so obtained are rathet too small for statistical analysis, for in some cases there are no figures for frequency of grooming at certain spatial positions. In spite of this, there is a clear positive correlation in all cases except Bird IV.

From these results I conclude that, with the exception of one individual bird, the main factor governing frequency of grooming is the time available. This is true for all three intensities of conflict. This suggests that variation inthe pattern

*Grooming almost never occurred on the ground during an 'approach'; the situation is entirely different from sitting on perch, and makes grooming very much more difficult to perform, especially such actions as bill wiping. As it is not comparable, this position has been omitted from this part of the analysis.

Table XI. Frequency of Grooming per Hundred Visits (G/100V), and Mean Length of Non-grooming Visit ($\bar{T}V^{-G}$), at Different Perches in Conflict Situations of Increasing Intensity.

Intensity of conflict (deprivation in minutes)	Perches:	1	2	3	4	5
a. All birds summed						
30	G/100V	6·2	11·2	2·8	1·8	10·0
	$\bar{T}V^{-G}$	0·038	0·040	0·033	0·021	0·051
75	G/100V	6·0	6·1	5·3	3·3	5·4
	$\bar{T}V^{-G}$	0·048	0·044	0·045	0·032	0·052
120	G/100V	8·3	8·1	3·5	7·5	8·5
	$\bar{T}V^{-G}$	0·058	0·053	0·046	0·041	0·067
b. Individual birds		Bird I				
30	G/100V	30·0	12·7	1·1	?	6·75
	$\bar{T}V^{-G}$	0·163	0·054	0·031	0·043	0·091
75	G/100V	?	7·8	5·8	2·3	3·2
	$\bar{T}V^{-G}$	0·050	0·073	0·040	0·038	0·069
120	G/100V	6·9	6·4	0·8	2·1	5·0
	$\bar{T}V^{-G}$	0·053	0·048	0·032	0·030	0·067
		Bird III				
30	G/100V	4·0	12·7	3·7	?	7·0
	$\bar{T}V^{-G}$	0·026	0·036	0·020	0·026	0·028
75	G/100V	2·0	6·2	6·9	4·5	5·3
	$\bar{T}V^{-G}$	0·023	0·032	0·033	0·030	0·035
120	G/100V	?	12·0	?	3·8	16·5
	$\bar{T}V^{-G}$	0·030	0·040	0·041	0·035	0·041
		Bird IV				
30	G/100V	19·5	28·5	14·2	14·3	7·7
	$\bar{T}V^{-G}$	0·065	0·063	0·101	0·058	0·069
75	G/100V	32·3	33·4	15·0	20·9	6·6
	$\bar{T}V^{-G}$	0·100	0·059	0·186	0·098	0·132
120	G/100V	30·2	?	25·0	22·3	17·4
	$\bar{T}V^{-G}$	0·141	?	0·062	0·077	0·142
		Bird V				
30	G/100V	5·9	3·6	?	?	37·5
	$\bar{T}V^{-G}$	0·032	0·025	0·092	0·042	0·117
75	G/100V	8·1	7·5	?	3·4	13·0
	$\bar{T}V^{-G}$	0·050	0·052	0·052	0·051	0·078
120	G/100V	9·4	14·3	?	2·2	23·9
	$\bar{T}V^{-G}$	0·083	0·050	0·076	0·054	0·116
		Bird VI				
30	G/100V	0·7	3·1	3·1	3·0	11·4
	$\bar{T}V^{-G}$	0·024	0·037	0·029	0·037	0·056
75	G/100V	1·1	?	1·4	1·1	4·0
	$\bar{T}V^{-G}$	0·028	0·032	0·035	0·030	0·047
120	G/100V	2·0	5·6	1·0	0·7	2·6
	$\bar{T}V^{-G}$	0·030	0·031	0·029	0·040	0·057

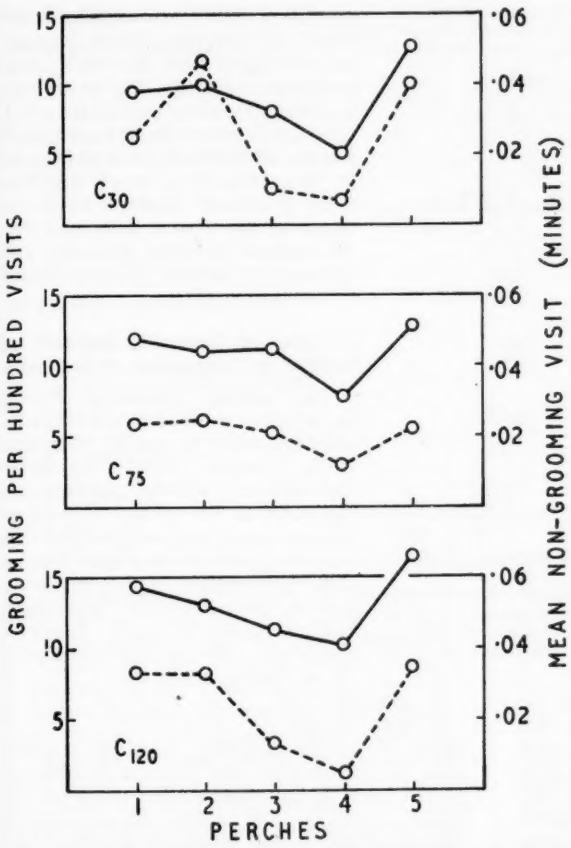


Fig. 11. Correlation between grooming (grooming bouts per hundred visits, broken line) and average length of non-grooming visit (solid line), at each perch in conflict situations of increasing intensity. Average of five individual performances.

ment produced by different degrees of deprivation and hence producing variation in the available time, is the cause of the observed variation in grooming.

From these correlations the length of visit at which probability of grooming approaches nil can be calculated, as described for the owl mobbing results on page 45. The results for the three conflict situations for the two birds which show the best correlation are:

Bird I 0·030 0·028 0·028 minutes.
Bird II 0·020 0·018 0·025 minutes.

The differences between levels of conflict are not significant, so that mean values are accepted:
Bird I 0·028 minutes. Bird II 0·021 minutes.

Fig. 12 shows the frequency distribution of grooming visits for these two birds; there is a sharp cut-off just about the calculated values. This agrees with the results of the same treatment of the owl-mobbing data (Fig. 5). Thus the minimum length of visit likely to contain grooming is rather longer in these experiments than in the owl-mobbing routine (0·017 minutes). This is probably due to a greater degree of disequilibrium necessary to terminate a visit under these conditions of transverse perches.

It is not possible to continue the analysis as was done with owl mobbing for the figures are insufficient to justify it. However, as far as I have gone, the results described show that precisely the same principles govern the occurrence of grooming in the hunger-fright conflict situation as in owl mobbing. Further, these effects can be demonstrated in the performance of most individual birds, as well as in the average of many.

5. Effect of Increasing Intensity of Conflict on Frequency of Grooming.

Previous experiments have shown that frequency of grooming changed in conflict situations of increasing intensity, and that these changes correlated with changes in the average length of visit. This suggests that the grooming behaviour is not directly influenced by the intensity of conflict at all, but only indirectly in that other types of behaviour, especially locomotion, are directly affected, which in turn alters the opportunity for grooming to occur. The owl-mobbing analysis showed that this opportunity could be usefully described (i.e. predictions could be made) as the time available at equilibrium to respond to peripheral stimulation.

The "surplus" hypothesis of displacement would suggest an increase in grooming with increase in conflict, other factors being the same. Van Iersel & Bol (1958) described such an effect, though they attributed it to different causes. Stated in terms of the mechanism proposed above, this requires that the frequency of grooming per visit per perch should increase with increasing intensity of conflict, even though the average length of non-grooming visit remained the same. However, Table XI shows that the average length of non-grooming visit does not remain the same, so one cannot merely make a

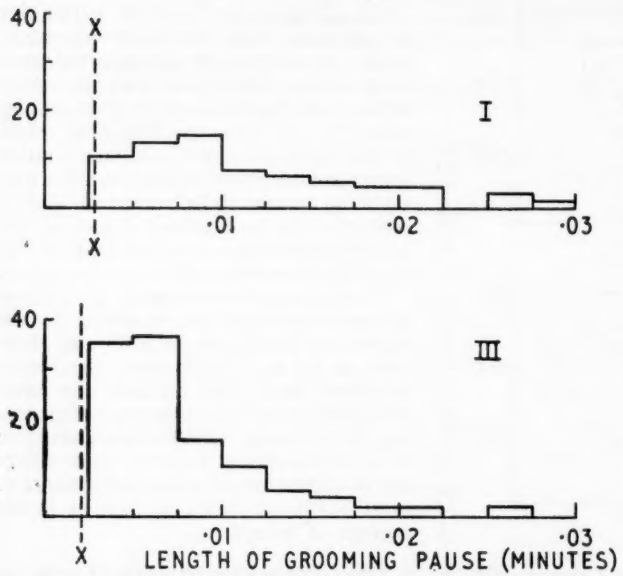


Fig. 12. Frequency distribution of grooming pauses of different lengths during hunger-fright conflict experiments. Individual records for birds I and III only shown. The broken lines X—X represent the calculated values at which the probability of grooming approaches nil (Bird I, 0.028 min., Bird III, 0.022 min.).

straight comparison of the figures for each intensity, but must first allow for the fact that the length of visit changes. The fact that the length of visit at which grooming is likely to be nil does not change significantly with conflict (p. 00) suggests that the effect is not present, but a more direct answer can be obtained mathematically, and I am indebted to Dr. K. E. Machin who suggested the method used. Table XIV gives the values of grooming per hundred visits and length of average non-grooming visit for the summed performance of all birds, which are (p. 00) significantly positively correlated. The surplus hypothesis would predict that the ratio of length of visit to frequency of grooming would decrease with increasing intensity of conflict. In Table XV this ratio is called α. First, it is obtained for each perch at each degree of conflict, and an average value for all perches is found for each degree of conflict. This average and its standard deviation are given in Table XII. Instead of showing a significant decrease, as theory would demand, they show a non-significant but continuous increase.

This means that far from causing a significant increase in grooming, the increase in conflict is associated with a non-significant decrease. This decrease, if real, is possibly associated with the much more pronounced decrease that occurs with deprivation without conflict (p. 58). I conclude therefore that the concept of increase in conflict causing an increase in "grooming drive" or of "displacement grooming" cannot be maintained in the present case, and that the relation between grooming and intensity of conflict is the incidental one suggested above.

6. Effect of Increasing Intensity of Conflict on Composition of Grooming.

The "surplus" hypothesis predicts an increase in intensity of displacement grooming as conflict increases. It is, however, difficult to define "intensity of grooming" satisfactorlly. van Iersel & Bol (1958) reported an increase in intensity of grooming with increasing conflict, and used 2 measures; the number of acts per bout, and the proportion of "high threshold" activities. To explain these they postulated that the disinhibition of the grooming centre is

a. stronger, and
b. lasts longer

when the conflict is strong. However, it seems that an increase in the time at equilibrium (=*b.* above) would alone suffice to explain the observed effects. The number of acts/bout is clearly related to the length of the bout, and would be expected to vary with available time in the same way as was demonstrated for acts of different length. It was in fact shown that "compound bouts" did vary in this way (Table XII). The "high-threshold" activities listed by these authors are the more complicated types of grooming, which take longer to perform. The absence of such a "high-threshold" activity is not necessarily an indication of a low level of peripheral stimulation or grooming drive (depending on definition of "threshold") unless it can be shown that opportunity is adequate at the moment of absence, and this is not usually possible.

My own experimental data is not adequate to analyse this effect in detail. However, a rough indication is possible in the following way.

The hypothesis is that the observed variation in composition of grooming is dependent upon

Table XII. Assessment of Change in Relationship Between Frequency of Grooming and Mean Length of Non-grooming Visit with Change in Intensity of Conflict.

α	Intensity	Perch: 1	2	3	4	5
(ratio of grooming/100 visits to mean length of non-grooming visit)	30	6·1	3·4	11·8	11·7	5·1
	75	8·0	7·3	8·5	9·7	9·6
	120	7·0	6·5	13·1	27·7	7·9

	Intensity: 30	75	120
Mean of α for all perches	7·6	8·6	12·4
S.D. of α for all perches	3·5	1·1	8·1

Comparison of different intensities:

Conditions compared	Difference	S.E. of difference	P.
30 & 75 min. deprivation	+1·0	1·6	<0·5
75 & 120 min.	+3·8	3·7	<0·3
30 & 120 min.	+4·8	3·1	<0·13

the average length of visit, in the manner described above. I will restrict my analysis to the four birds (I, III, V & VI) that show a good correlation between frequency of grooming and length of visit, as only here would the effect be expected. Then, lumping these four birds together, it can be calculated from the data given in Table XI that the average length of visit in the different conflict situations is as shown in Table XIII; that is, it is shortest after 30 minutes deprivation, and after both 75 and 120 minutes is rather longer. The shortest grooming action is a single bill wiping act. Table XIII also gives the proportion of the total grooming recorded for these birds which is composed of single bill wiping acts. It can be seen that when the visits are on the average shortest, there is the highest proportion of this very short action. This is in agreement with the hypothesis.

Now bill wiping is not only the shortest grooming action but in the terms of van Iersel & Bol (1958) or the model given in the Appendix, it also has the lowest threshold. Thus it is true for these four birds that they show a greater proportion of high threshold grooming at higher intensities of conflict; but such a statement would obscure the fact that this distribution is expected any way, irrespective of threshold differences, on the basis of variation in available time. The present experimental results therefore do not support the view that changes in intensity of conflict have a direct effect upon the intensity of grooming observed.

Table XIII. Association Between Average Length of Visit and Probability of Occurrence of Single Bill Wiping acts, in Conflict Situations of Increasing Intensity.

	Intensity of conflict (deprivation in minutes)		
	30	75	120
Proportion of total grooming bouts which consists of one bill-wiping act	52%	45%	45%
Total no. visits	272	201	183
Total time spent in visits	11·26	10·45	8·92
Mean length of visits	0·042	0·050	0·049 minutes

V. Grooming in Non-conflict Situations After Deprivation of Food.

The previous experiments with hunger-fright conflict situations involved different degrees of deprivation. It is possible that some of the effects attributed to increase in conflict could be caused instead by increase in deprivation. In order to test this possibility, a series of experiments were performed under identical conditions as the hunger-fright conflict series, with the difference

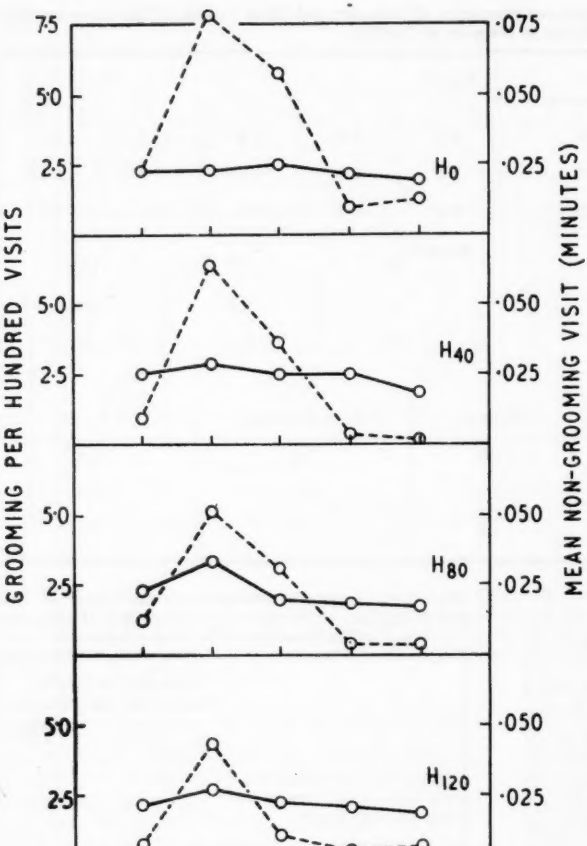


Fig. 13. Relation between grooming (grooming bouts per hundred visits, broken line), and average length of non-grooming visit (solid line), at each perch in hunger situations after increasing deprivations. Average of six individual performances.

that after a period of deprivation behaviour was recorded for ten minutes without the food-dish being returned. Four periods of deprivation were examined, of nil, forty, eighty and one hundred and twenty minutes. Six birds were used, and each was tested ten times in each situation.

The summed results of all the birds are shown in Table XIV. From this, it can be seen that with increasing deprivation

(*a*) the time spent sitting on perches progressively decreases,

(*b*) there is a slight over-all increase in the frequency of visits to perches, and therefore

(*c*) the average length of visit to the perch progressively decreases,

(*d*) foraging increases steadily, as measured by both the number of bouts and the total time spent,

(*e*) time spent flying is least when deprivation is least,

(*f*) there is a steady decrease in the frequency of grooming bouts, both as uncorrected totals, and when expressed per hundred visits.

All these differences are significant. The same trends, though not always significant, are present in the average results all individual birds.

In conflict situations there is a correlation between the length of visit and the frequency of grooming. If this is also here, then possibly the decrease in grooming is due to the decrease in average visit length. The frequency of groomingper hundred visits is shown for each perch, and also the average length of non-grooming visit, are shown for all birds summed in Fig. 13. In the conflict situation these two measures are strongly positively correlated. In this case both plots have characteristic shapes for each individual, which do not vary much with deprivation. There is, however, no trace of correlation between the two. This then is a fundamental difference between the relations of grooming and locomotion in conflict and hunger situations. Further, the average length of non-grooming visit per perch varies little or not at all with increasing deprivation,* while the frequency of grooming steadily declines. This means that the length of visit is not the main immediate factor controlling grooming, as in the conflict situations, and further, that some other factor is causing a steady decrease of grooming with increasing deprivation.

Without further experiment, the cause of this decrease can only be speculated upon. Changes

*There is no contradiction between the fact that the average length of all visits to all perches declines with increasing deprivation, while those to individual perches remain constant. This merely implies that with deprivation the bird makes more visits to those perches which have the shortest average visit; this can in fact be demonstrated.

Table XIV. Comparison of Behaviour After Progressive Deprivation.

	Deprivation in minutes 0	40	80	120	
Total time on perches	442	395	379	377	minutes
Total no. visits to perches	10140	10360	9920	10660	
Mean length of visit	0·044	0·038	0·036	0·035	minutes
Total no. foraging bouts	144	184	219	287	
Total time spent foraging	30·3	42·5	67·5	74·7	minutes
Time spent flying	129·8	163·6	153·6	150·0	minutes
Frequency of grooming bouts	478	330	273	236	
Grooming per hundred visits	4·70	3·19	2·75	2·21	

in neither peripheral stimulation nor available time seem adequate, so presumably some motivational change takes place with increasing deprivation. Whatever the reason, it is clear that the hunger-fright conflict and the simple deprivation situation are fundamentally different, and the results of the former cannot be due to the necessary presence of the latter within it.

VI. Discussion

The "surplus" hypothesis of motivation was rejected by van Iersel & Bol (1958) and Sevenster (in press). The former authors produced experimental evidence showing that displacement grooming was associated with approximate equality or equilibrium between the tendencies involved in the primary conflict. They also showed that when the bird was engaged in only one of the activities involved in the conflict situation, grooming occurred infrequently.

From these observations they concluded that inhibitory relations existed between grooming and each activity of the primary conflict. In conflict, mutual inhibition of these two primary activities occurs, thus decreasing the inhibition each exerts on grooming, which is therefore more likely to appear. This explanation is clearly an enormous advance on the "surplus" hypothesis. Especially, it accounts for displacement activity in terms of the probability of other activities ("effective equality") and the displacement activity's own "positive factors". These "positive factors" ("the resultant of internal and external excitatory factors") are basically the same for all occurrences of grooming. However, this theory of causation appears incomplete in that these other positive factors are not analysed further, but are considered a relatively constant source, the expression of which in conflict situations is regulated by the degree of disinhibition produced by the conflict, which thus produces the variation in grooming observed in different circumstances. Such an interpretation has many of the disadvantages of unitary drive concepts (cf. Hinde, 1959) and particularly, by minimizing the role of peripheral stimulation and the effect of grooming on it, does not provide a stimulus response feedback loop synchronizing behaviour with environment, and thus largely deprives grooming of functional significance.

The experiments with Chaffinches confirm that displacement grooming correlates with equilibrium, i.e. equality of the two primary conflict tendencies, and that the primary conflict tendencies, when not in conflict, correlate with a low frequency of grooming. These observations can be adequately described in terms of disinhibition of grooming at equilibrium, though it is doubtful whether this description can be considered a theory of causation. However, once granted the importance of the equilibrium state, the observed variation in grooming correlates not with the "degree of disinhibition", but with two other measures, intensity and type of peripheral stimulation, and available time, i.e. duration of the equilibrium state. These correlations are good enough to justify the view that equilibrium in conflict situations is a simple permissive, on-and-off factor governing the appearance of a third type of behaviour, and that the nature of the observed grooming is

primarily a function of these other two factors.

This theory has certain advantages, apart from agreeing better with the Chaffinch data. By substituting the combination of peripheral stimulation and inhibition by other activities for grooming drive, one loses some intervening variables, provides a feedback loop between stimulus and response, and suggests a plausible method of linking grooming with its biological function, care of the body surface. Further, if this sytem is accepted it seems that intensity of conflict does not affect the nature of the equilibrium state, nor directly any factor controlling displacement activity. This requires much less complex machinery between input and output in the CNS than do other explanations.

In the Introduction I pointed out that the unique property of displacement activities was their timing; why does the bird groom just then, rather than continue with the conflict actions? Van Iersel & Bol (1958) suggested an explanation and this paper has elaborated on it, but it is of course only one example of the theoretical difficulties of initiating any one type of behaviour, faced with a huge sensory input which could lead to many. One can in fact show that many types of behaviour, never normally associated with "displacement", have a precisely similar background, in that they occur regularly at the transition between two types of mutually incompatible behaviour.

For example, on winter afternoons Chaffinches have a monotonous cycle of behaviour about 20 minutes long with two main features; sleep or rest on a perch, and feeding on the ground. Grooming occurs here

(*a*) after feeding, before settling down to rest, when it is presumably responding mainly to stimulation caused by feeding, as it consists mainly of cleaning the bill and feet;

(*b*) on 'waking up,' immediately before commencing the locomotion which leads to feeding. Here the grooming is of a more diverse nature than in (*a*).

In the latter case especially, it seems that grooming is a response to a normal level of peripheral stimulation, occurring at the transition between two incompatible types of behaviour, both of which exclude grooming. Except that the whole time scale is less rapid, the situation is thus exactly comparable to grooming occurring between advance and retreat in an approach-avoidance conflict. Because of the slower time-scale, however, this would never strike the observer as "displacement activity". Thus it appears that displacement activity is at best merely an extreme case of a general principle.

These arguments suggest that displacement activities will be "background motivations" showing through, as it were, when the normally stronger ones cancel each other out. Apart from maintenance activities such as grooming, the other big class of reported displacements are "inappropriate" types of sexual or reproductive behaviour. Now the reproductive cycle of birds consists of a number of different activities, whose frequency of occurrence changes progressively through the season (e.g. Hinde (1958), Canaries). Very probably the causal factors for most of the different kinds of behaviour are present at low level throughout, both before and after their peak times of occurrence; the frequency curves have long "tails". Thus, for example, Baggerman *et al.* (1956) explained courtship feeding by male *Chlidonias niger* as weakly motivated feeding of nestlings occurring when the female presented favourable releasing stimuli. Thus it would seem that these sexual and reproductive displacement activities would fit the same sort of explanation as the mainteance activities.

The behaviour originally described by Tinbergen (1940) as "displacement activity" is seen to be a heterogeneous category, whose main common feature is this at first puzzling response to what is apparently one of the weaker stimuli presented by the environment. "Vacuum activity" and "redirection activity" have been recognized as different from the behaviour which typically occurs in conflict situations (Bastock, Moynihan & Morris, 1953). Andrew (1956) and Morris (1956) have shown that some "displacements" are probably the results of autonomic nervous activity produced directly or indirectly in conflicts. Lind (1959) elaborating on earlier proposals by Tinbergen (1952) and others, shows that an animal motivated to perform a behaviour A, and less strongly to perform a behaviour B, may switch to B in the middle of A if an action common to both (a "transitional action") occurs. In the right circumstances, this can give an appearance of irrelevance and be labelled displacement. Further, the term was loosely extended to cover many types of behaviour where the normal causal factors were certainly present at the time of occurrence (Moynihan, 1955). The present analysis shows that this is abundantly true of grooming in conflict situations. Displacement grooming has the normal causal factors, and its unusual features are due solely to differences in opportunity to occur in conflict and other situations, differences which are in themselves in no way absolute.

APPENDIX

Grooming after Bathing, and the Threshold Values of Different Kinds of Grooming.

The periods of grooming which are longest and contain the greatest variety of actions occur in undisturbed periods following bathing. Immediately bathing occurs, the plumage is thoroughly draggled and wet, and peripheral stimulation must be at its maximum. Grooming after bathing was recorded in 20 individuals kept singly in outdoor aviaries, and is analysed below.

1. Relative Frequency of Different Grooming actions in the Total Period.

The commonest grooming actions are, in order of decreasing frequency;

bill wiping,
feather settling,
scratching.
preening of different parts of the body; the relative frequency for the different parts agrees with that obtained by van Iersel & Bol (1958).

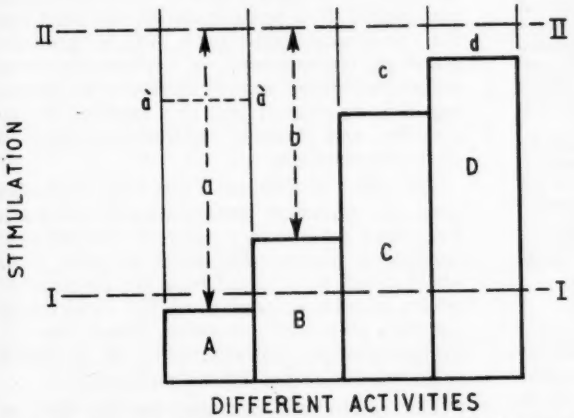


Fig. 14. Schematic diagram of the stimulation required to elicit four grooming activities, A, B, C, and D, of progressively higher threshold. For further explanation see text.

The first two, bill wiping and feather settling, are by far the most common, usually making up more than half the total grooming recorded.

2. Relative Frequency of Different Grooming Actions in Successive Time Units after Bathing.

If grooming after bathing is grouped into totals for successive 30 seconds periods, the frequency of grooming (all movements summed) is highest immediately after the end of bathing, and declines in successive units (Table XV). The relative frequency of the different types of grooming shows definite sequential changes. Preening movements, virtually absent at the start of grooming, rise to a peak about a third of the way through the total period, and die away again towards the end. At the beginning and end of the period, grooming is almost exclusively composed of the simpler types of movement, bill wiping, feather settling, and scratching. Similar results were obtained by van Ierel & Bol (1958). They concluded that this sequence indicated a sequential change in grooming drive, and that the different types of grooming had different drive thresholds. Threshold differences are not, however, the only possible explanation for such a result; for example, all the actions could have the same threshold, but differ in their latency, which could result in the actions with the lowest latency appearing more frequently (I am indebted to Dr. R. A. Hinde for this suggestion). If, however, threshold differences are accepted as a probable cause of the observed sequences, it is not necessary to postulate drive thresholds or drive variations, for if the following assumptions are accepted:

1. Grooming is a response to external stimulation;
2. the different types of grooming have different thresholds (of stimulation);
3. the act of grooming decreases the stimulation producing it,—then the observed sequence of grooming follows automatically.

Thus, in Fig. 14 the different threshold values are shown diagrammatically, where activities A-D have successively higher threshold values (=amount of stimulation needed to elicit them). If the level of stimulation is that indicated by line I, only activity A can appear. If the level is that of line II, all types of activity should appear, unless prevented by some other factor. There are two possible ways in which they could appear. First, if the response was of the all-or-nothing type, the different actions would be expected first with equal frequency, and each would begin the sequence on an equal number of occasions. If, on the contrary, the response was graded—that is, related in intensity to the amount of stimulation present above threshold—then the activities with low thresholds would be the first to appear. As Table (XV) shows, there is a well defined order of appearance, so the latter alternative must be accepted. The first to appear—and the commonest ones—are bill wiping and feather settling. On these grounds these would be the lowest in threshold.

Accepting postulates 1 and 3, and the arguments for a graded response, it follows that the change-over between one activity and the next (say A and B) occurs when the level of stimulation eliciting A fails sufficiently beneath that eliciting B; i.e. when on diagram the quantity 'a' falls beneath the quantity 'á'. Quite possibly it must fall

Table XV. Grooming in Successive 30-second Periods After Bathing has Ceased (average of 20 observations).

Time after bathing	0/30	31/60	61/90	91/120	121/150	151/180	181/210	211/240
Total no. grooming acts	14	12	12	12	12	7	6	3
Total no. of preening acts	0	2	9	5	4	2	0	0

well beneath that level, but this does not affect the argument. After change-over to B has occured, that type of stimulation will decrease (postulate 3) until one of two things happens. Which depends on the relative values of the thresholds of A and C. In either case, b. will fall until it is either appreciably less than 'á'—in which case there will be a change back to A, and the cycle starts again—or appreciably less than c, in which case there will be a second change to activity C.

In this way, there will be an overall trend with increasing time from low to high threshold activities, but a trend that may often be interrupted and temporarily reversed en route, depending on the characteristics of the system and on secondary changes in stimulation—e.g. some activities like shaking may decrease the stimulation over many areas of the body. However, when the highest threshold is finally reached this is not the end of the sequence, as there is still stimuli left eliciting low threshold activities, and the bird will revert to these. The last activities performed will be the ones with lowest thresholds. This is precisely what occurs in undisturbed sequences after bathing, and to this extent the model is a useful one. If it is accepted, the order of increasing threshold of grooming activities will be the order of decreasing frequency of occurrence given above (p. 61).

This is in fact the order of frequency in which grooming appears under all conditions (e.g. the conflict experiments described in this paper) which do not involve particular stimulation of one area of the body. This is in further agreement with the postulates listed above.

However, it seems that the stimuli required to elicit the different kinds of grooming are qualitatively different, at least in as much as they concern different areas of the body. Unless it could be shown that all the inputs were similar (and not even the receptor organs for any are known at present), then there is some logical difficulty in arranging qualitatively different stimuli on a single threshold scale.

VIII. Summary

An attempt is made to explain displacement grooming in approach-avoidance conflict situations on the assumption that grooming is a response to peripheral stimulation. Local and general increases in peripheral stimulations produce specific and general increases in grooming in conflict and non-conflict situations. It is concluded that frequency and composition of grooming in conflict situations are initially determined by intensity and pattern on peripheral stimulation. However, this grooming is further regulated by the opportunity to respond to the stimulation. This can be subdivided into two parts:

1. A suitable state of motivation with respect to other activities. This is shown statistically to correlate with equal tendency to perform both the actions of the primary conflict. This is called the equilibrium state.

2. Duration of the equilibrium state—i.e. adequate time at equilibrium to perform the grooming response. Thus when stimulation is constant in conflict situations, probability of grooming is directly proportional to the average length of visit at any point; thus the controlling factor is the probability of interruption. The different grooming actions are associated with pauses of different lengths, the components of which are analysed; the lengthiest types are most susceptible to interruption, and are therefore least frequent where visits are shortest. There is thus a "mechanical" effect on the composition of grooming, independent of the initial pattern of peripheral stimulation. There is a minimum length of time in which grooming can occur, which varies with different types of grooming, but which is always longer than the actual motor pattern. It is concluded that it is necessary for the bird to remain in the equilibrium state for a certain period before grooming commences. It is possible during this time that the peripheral stimulation which produces grooming is perceived. As interruption is the main controlling factor of displacement grooming, it is considered that this explains the incomplete and "frantic" performance which is often characteristic.

The effect of different intensities of conflict upon the grooming performance is examined. Grooming performance differs in the different conditions, but the differences are only those which could be expected from the direct effect of the increase in conflict on the incidence of activities other than grooming. When these are compensated for mathematically, the grooming performances do not differ significantly.

The results are discussed in the light of theories of motivation of displacement activity. No evidence for the "surplus" hypothesis has been found. It is confirmed that disinhibition of grooming takes place at equilibrium in conflict situations, but the further control of frequency and composition is due to the factors described, not the degree of disinhibition.

Acknowledgments

I am grateful to Drs. R. A. Hinde and T. E. Rowell for criticism of the manuscript, to them and Drs. W. H. Thorpe, N. Tinbergen, A. C. A. Bol and P. Sevenster, for discussion of the subject in general, and to Dr. K. E. Machin for advice on statistical treatment. The work described was performed while the author held an Agricultural Research Council research scholarship.

REFERENCES

Andrew, R. J. (1956a). Some remarks on behaviour in conflict situations, with special reference to *Emberiza* spp. *Brit. J. anim. Behav.*, **4**, 85-91.

Andrew, R. J. (1956b). Normal and irrelevant toilet behaviour in *Emberiza* spp. *Brit. J. anim. Behav.*, **4**, 41-45.

Armstrong, E. A. (1950). The nature and function of displacement activities. *Symp. Soc. exp. Biol.*, **4**, 361-386.

Bastock, M., Morris, D. & Moynihan, R. (1953). Some comments on conflict and thwarting in animals. *Behaviour*, **6**, 66-84.

Baggerman, B., Baerends, G. P., Heikens, H. S. & Mook, J. H. (1956). Observations on the behaviour of the Black Tern (*Chlidonias n. niger* (L.) in the breeding area. *Ardea*, **44**, 1-71.

Hartley, P. H. T. (1950). An experimental analysis of inter-specific recognition. *Symp. Soc. exp. Biol.*, **4**, 313-336.

Hinde, R. A. (1954a). Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the Chaffinch (*Fringilla coelebs*). *Proc. roy. Soc. B.*, **142**, 306-358.

Hinde, R. A. (1954b). Changes in responsiveness to a constant stimulus. *Brit. J. anim. Behav.*, **2**, 41-53.

Hinde, R. A. (1955). A comparative study of the courtship of certain finches (*Fringillidae*). *Ibis*, **97**, 706-745.

Hinde, R. A. (1956). Ethological models and the concept of 'drive'. *Brit. J. Phil. Sci.*, **6**, 321-331.

Hinde, R. A. (1958). The nest-building behaviour of domesticated canaries. *Proc. zool. Soc. Lond.*, **131**, 1-48.

Hinde, R. A. (1959). Unitary Drives. *Brit. J. anim. Behav.*, **1**, 130-141.

van Iersel, J. J. A. & Bol, A. C. A. (1958). Preening in two tern species. A study of displacement activities. *Behaviour*, **13**, 1-88.

Kennedy, J. S. (1954). Is modern ethology objective? *Brit. J. anim. Behav.*, **2**, 12-19.

Kennedy, J. S. (1958). The experimental analysis of aphid behaviour and its bearing on current theories of instinct. *Proc. 10th int. Congr.*, Montreal, 1956, **2**, 397-404.

Kortlandt, A. (1940). Wechselwirkung zwischen Instinkten. *Arch. neerl. Zool.*, **4**, 442-520.

Lehrman, D. S. (1953). A critique of Konrad Lorenz's theory of instinctive behaviour. *Quart. Rev. Biol.*, **28**, 337-363.

Lind, H. (1959). The activation of an instinct caused by a "transitional action". *Behaviour*, **14**, 123-135.

Marler, P. (1952). Variation in the song of the Chaffinch (*Fringilla coelebs*) *Ibis*, **94**, 458-472.

Marler, P. (1955-56). Studies of fighting in Chaffinches. *Brit. J. anim. Behav.*, **3**, 111-117, 137-146; **4**, 23-30.

Marler, P. (1956a). Behaviour of the Chaffinch (*Fringilla coelebs*). *Behaviour*, Supp. V.

Marler, P. (1956b). The voice of the Chaffinch and its function as a language. *Ibis*, **98**, 231-261.

Morris, D. (1956). The feather postures of birds and the problem of origin of social signals. *Behaviour*, **9**, 75-114.

Moynihan, M. (1955). Remarks on the original sources of displays. *Auk*, **72**, 240-246.

Rand, A. L. (1941). Development and enemy recognition of the curve-billed thrasher, *Toxostoma curvirostre*. *Bull. Amer. Mus. nat. Hist.*, **78**, 213-242.

Schmidt, H. D. (1956). Das Verhalten von Haushunden in Konflikt-situationen. *Z. Psychol.*, **159**, 162-245.

Sevenster, P. (In Press).

Thorpe, W. H. (1951). The definition of terms used in animal behaviour studies. *Bull. anim. Behav.*, **9**, 34-40.

Tinbergen, N. (1940). Die Übersprungbewegung. *Z. Tierpsychol.*, **4**, 1-40.

Tinbergen, N. (1950). The hierarchical organisation of nervous mechanism underlying instinctive behaviour. *Symp. Soc. exp. Biol.*, **4**, 315-372.

Tinbergen, N. (1952). "Derived" activities; their causation, biological significance, origin, and emancipation during evolution. *Quart. Rev. Biol.*, **27**, 1-32.

Tugendhat, B. (1959). Studies on the effects of thwarting in Sticklebacks. Dissertation for degree of Doctor of Philosophy in the University of Oxford.

Accepted for publication 13*th June*, 1960.

ROLES OF THE MALE AND THE NEST-CUP IN CONTROLLING THE REPRODUCTION OF FEMALE CANARIES

By ROSLYN P. WARREN* and R. A. HINDE

Sub-department of Animal Behaviour, Madingley, Cambridge

Introduction

Reproduction in a seasonally breeding bird depends in part on stimuli from the physical environment which influence gonad development by a pituitary mechanism (Rowan, 1931; review by Marshall, 1959). It is also influenced by stimuli from the biological environment, including products of the bird's own activities, such as nest, eggs, etc. (review by Lehrman, 1959). In a previous paper it was shown that, in domesticated canaries, stimuli from the nest-cup accelerate egg-laying (Hinde & Warren, 1959). The aim of the present study was to assess the influence of the male on the female's reproductive development, and to determine the stage in the reproductive cycle at which it is exerted.

Material and Methods

(1) *Stock*. The canaries used, of the Border variety, were obtained from dealers in the late winter of 1958/59 and were believed to be first year birds.

(2) *Procedure*. All birds were introduced to the experimental cages on March 18th. Most of them were placed in enamelled metal cages 110 cm. × 35 cm. × 30 cm. as described elsewhere (Dunnett & Hinde, 1958). Four pairs were put into cages, constructed of ½"-mesh galvanized wire netting, with hemispherical floors designed so that no corners or crevices could provide stimuli similar to those provided by a nest-pan (see Hinde & Warren, 1959).

The birds were divided into groups as follows:

Group I A. Kept in the enamelled metal cages in pairs (male and female). A standard plastic canary nest-pan, and superabundant nest material consisting of dried grass and feathers, were present continuously from March 24th. These conditions were similar to those of Group I in the previous study. (8 pairs).

Group I B. Kept in the enamelled metal cages in pairs. A standard plastic canary nest-pan was provided continuously, but nest material was provided only for the duration of three ten-minute watches each week. After each watch all material was removed from the nest-pan and cage. These conditions were similar to those of Group III in the previous study. (7 pairs.)

Group I C. Kept in the round-bottomed cages in pairs, and provided with material only for the duration of three ten-minute watches weekly. The conditions were similar to those of Group IV in the previous study. (4 pairs.)

Group II A. Females kept in enamelled cages, visually but not auditorally isolated from males. A standard canary nest-pan and superabundant nest material were present continuously from March 24th as in Group IA. (Initially 8 birds but 2 of these later proved to be males.)

Group II B. Females kept in the same conditions as Group II A, but without a nest-pan or nest material. (5 birds.)

In summary, the females in Groups I A, I B and I C were paired with males, while those in Groups II A and II B were visually isolated from them. The A, B and C sub-groups differed in the amount of stimulation they could obtain from a nest-pan as in the previous study.

(3) *Data recorded*. The effect of the various group treatments on the following aspects of reproductive development were assessed:

(i) Start and (ii) completion of defeatherisation of the brood-patch. In passerine birds, brood-patch development involves externally visible changes of three sorts—loss of feathers from the ventral surfaces, increased vascularization of these surfaces, and oedema (Bailey, 1952; unpublished observations). Marked changes in vascularization and the occurrence of oedema are limited to the days immediately preceding and succeeding egg-laying: in the present study only the defeatherisation was assessed, the dates of its completion being recorded. Unfortunately the start of defeatherisation had already occurred in most individuals by the time of the first examination.

(iii) Start and (iv) completion of nest-building. For present purposes, the date of the beginning of effective building was recorded, as well as, in Groups IA and IIA, that of the completion of

*Now at Howard University, Washington, D.C.

the nest. Since the tempo of nest-building behaviour differs between females provided with materials constantly and females provided with material only during limited watches (Hinde, 1958), the criterion used differed between groups. For Groups I A and II A, effective building was deemed to have started when two or more pieces of nest material (grass or feathers) were found in the nest-cup. Placing of material by males is relatively rare, but in each case observation of the birds confirmed that the females were building. In Group I B the day on which the female was first seen to place material in the cup during one of the thrice-weekly watches was taken as the start of building. In Group I C, for whom placing of material was made impossible by the absence of a nest-site, three bouts of carrying material in a watch was taken as the criterion. (For more detailed descriptions of these activities, see Hinde, 1958.)

(v) *Egg-laying.* All cages were inspected daily for eggs. The date of the first egg and the clutch size was recorded.

(vi) *Incubation.* Not all birds incubate the eggs which they lay. The occurrence of incubation within 6 days of egg-laying was recorded.

Observations were continued until June 15th.

Results

The principle results are summarized in Fig. 1.

(i) *Start of defeatherisation.* Nearly all birds showed some signs of defeatherisation when the first examination was made on April 10th. Comparisons of the number of females showing no defeatherisation on this date between the groups in which males were present (1 out of 19) and the groups in which no males were present (2 out of 11), or between groups in which nest pans were present (1 out of 21) and those in which they were not (2 out of 9) showed no significant differences.

(ii) *Completion of defeatherisation.* Defeatherisation was completed in all the Group I A birds by April 18th, with the exception of one bird in which it was delayed until May 23rd. Completion of defeatherisation in Groups IB and I C was delayed, but occurred in 6 out of 7 Group I B birds by May 13th and in all four Group I C birds by May 29th. The median dates of completion for Groups I A, I B and I C were April 6th, 28th and May 2nd respectively. (Differences between Groups I A and I B, I A and I C, significant at $P<0{\cdot}05$ by Mann-Whitney U test).

Of the Group II females kept without males, defeatherisation was not completed within the observation period in 2 out of 6 birds in Group II A and 2 out of 4 in Group II B. The median dates for the whole groups were May 19th and after May 20th respectively. (Differences between Groups I A and II A, I B and II B, significant at $P<0{\cdot}05$).

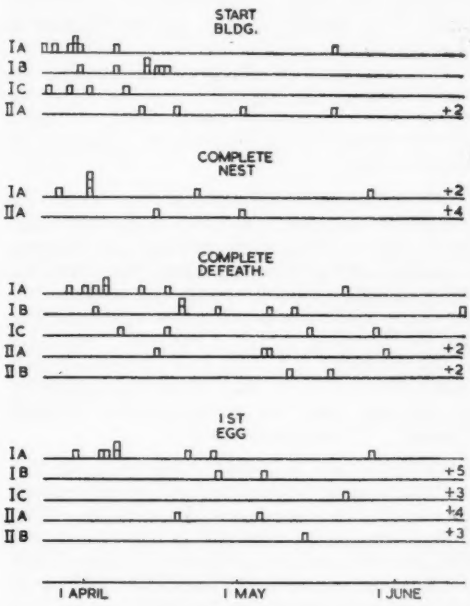


Fig. 1. Dates of the start of building, completion of the nest, completion of defeatherisation and laying of the first egg for Groups I A-C and II A and B. Figures on the right indicated the number of individuals which did not reach the criterion.

In summary, the completion of defeatherisation of females in both Group I and Group II was delayed by absence of facilities for nesting; and was later in the Group II birds, kept without a male, than in the Group I birds which were paired.

(iii) *Start of nest-building.* All the Group I birds (confined with males) showed some effective building behaviour by April 17th, with the exception of one bird in Group I A. The median dates for Groups I A, I B and I C were March 31st, April 14th and April 1st. Since, as explained above, the criteria used for the start of building could not be quite the same in these

groups, these figures cannot be taken to suggest a difference between them in the date at which the females were in a condition to start building.

Of the Group II A birds, two showed no effective building up to the end of the observations. The median date for the whole group for the start of building was May 12th. This certainly indicates a difference from Group I A ($P<0{\cdot}01$): indeed none of the six Group II A birds started to build until after 7 out of the 8 Group I A birds. Nest-building could not be studied in Group II B.

Thus the start of effective nest-building occurred later in the isolated females than in the paired females, but there was no evidence that it was influenced by the presence of a nest-pan or nest-material.

(iv) *Completion of nest-building.* Only the females in Groups I A and II A had opportunity to complete a nest. In fact, 6 out of the 8 Group I A birds built a substantial nest, the other two laying in rather sketchy nests. The median date for the 6 which completed nests was April 3rd, and for the whole Group April 14th. Only 2 out of the 6 females in Group II A completed nests (April 16th and May 3rd). Thus the completion of the nest also was delayed in the isolated females.

(v) *Egg-laying.* All of the birds in Group I A laid, the median date of the first egg being April 8th and the last two April 27th and May 28th. Only 2 females in Group I B laid (April 28th and May 7th) and one in Group I C (May 23rd). (Differences between Groups IA and I B, I A and I C significant at $P<0{\cdot}001$ and $P<0{\cdot}01$ respectively). The absence of nesting facilities thus adversely affected egg-laying, the effect being even more severe than in the previous study. Amongst the Group II females, only two from Group II A (April 20th and May 6th) and one from Group II B (May 15th) laid. (Difference between Groups I A and IIA significant with $P<0{\cdot}01$). Thus absence of a male was also associated with a delay in egg-laying. Since the proportion of paired females without adequate nesting facilities which laid (Groups I B and I C, 3 out of 11 birds) was little greater than the proportion of isolated females without nesting facilities (Group II B, 1 out of 4 birds), the influence of the male may be indirect, and consequent upon the presence of a nest (see Hinde & Warren, 1959).

For reasons not understood, clutch sizes were small—the initial clutch of all females which laid consisted of one egg except for one bird in Group I A (3 eggs) and one in Group II B (2 eggs).

(vi) *Incubation.* Of the birds in Groups I A and I B which laid eggs, 5 out of 10 incubated. The birds in Group I C were of course unable to incubate. Two of the 3 birds in Groups II A and II B which laid also incubated. There is thus no evidence that the presence of a male influences the occurrence of incubation once the eggs are laid.

Of the birds in Groups I A and II A (i.e. those able to build nests), 7 out of 10 incubated: two of the three birds which failed to incubate had built rather inadequate nests. Of the birds not able to build nests (Groups I B and II B), 0 out of 3 incubated their first clutch.

(vii) *Relation between the occurrence of nest-building, defeatherisation and egg-laying.* In order to assess the stage of the breeding cycle at which the male and stimuli from the nest-cup exert their effects, the proportion of birds passing from certain stages of reproductive development to the next, and the time intervals between these stages, were assessed.

(*a*) Interval between the start of nest-building and the completion of defeatherisation. In the control group I A the median interval was 6 days (range 4-17). It was longer in all other groups (I B, median 7, range 2-76; I C median 33, range 6-64; II A median 20, range 3-24+. Differences between I A and I B, I A and I C, significant with $P<0{\cdot}05$). The longer intervals shown by the groups which were deprived of nest-pans and/or nest material indicate that stimuli from the nest-cup influence the completion of defeatherisation. The difference between groups I A and II A, though not significant here, may have been also due to the same factor. Thus we have already seen that the nest-building behaviour of the isolated birds was reduced: and further, the intervals for the two birds which did complete nests (3 and 17 days) were within the range of the Group I A birds, suggesting that once the nest is built the presence of the male does not affect this interval significantly.

(*b*) Interval between the completion of defeatherisation and egg-laying. In Group I A all birds completed defeatherisation and laid eggs, the median interval being 3·5 days (range 0-14). In Groups I B and I C only 3 of the 11 birds which completed defeatherisation laid eggs, and here the delays were 0, 24 and 35 days.

Stimuli from the nest are thus important also at this stage. Amongst the isolated females, only 3 of the 6 which completed defeatherisation laid eggs: the failure of the others to lay was again probably not due directly to the absence of the male but to the consequent reduction in stimuli from the nest-cup. Thus the only 2 birds in Group II A which laid were also the only 2 to build a complete nest. Further, the intervals between completion of defeatherisation and egg-laying for these 2 birds were 1 and 4 days, indicating that if a nest is built the absence of the male does not significantly increase the interval.

Discussion

This study provides no evidence about the influence of the male or of nesting facilities on the start of defeatherisation. Since all females had been confined within sight of males before their introduction into the experimental cages, it is possible that there had been some effect before the experiment started: alternatively, the beginning of defeatherisation may be solely a consequence of increasing day-length and temperature.

There is, however, clear evidence that the presence of a male accelerated the occurrence of nest-building, the completion of defeatherisation and egg-laying. The 3 birds which laid in Groups II A and II B show that nest-building and egg-laying can be completed without a male, but these females may have been influenced by auditory stimuli: the sound of males is known to have an effect in Budgerigars (Vaugien, 1951; Ficken, van Tienhoven, Ficken & Sibley, 1960).

The data suggest that the influence of the male in accelerating the female's reproductive development is principally of importance up to the time of nest-building. Since the peak of copulation occurs 1-3 days before egg-laying (Hinde, 1958), and there are few successful copulations more than 5 days before, the influence of the male on the female's reproductive development is probably exerted through means other than copulation and the displays which immediately precede it.

This study also confirms that the presence of nest-building facilities influences the female's reproductive development. In fact the differences in egg-laying dates between Groups I A, I B and I C were even more marked than those between the corresponding groups in the previous study. Here the data suggests that stimuli from the nest, unlike those from the male, are important even after defeatherisation is complete. The influence of the male on egg-laying is thus exerted through the nest which he has been instrumental in causing the female to build.

In summary, then, these data indicate that stimuli from the male affect the occurrence of nest-building in the female. Stimuli from the nest influence the completion of defeatherisation and egg-laying (see also Hinde & Warren, 1959). There is also an indication that stimuli from the nest increase the probability of incubation, though such a relationship did not appear in the previous study. Evidence that stimuli from the nest also influence the tempo of building behaviour, the cessation of building and the selection of material have been presented previously (Hinde, 1958).

Summary

1. The influence of the male and of nesting facilities on the progress of the reproductive cycle of female canaries in spring was assessed.

2. Stimuli from the male may influence the start of defeatherisation and certainly influence the occurrence of nest-building in the female. Stimuli from the nest influence defeatherisation and egg-laying.

Acknowledgments

This study was supported by a grant from the United States Air Force Biosciences Division.

REFERENCES

Bailey, R. E. (1952). The incubation patch in passerine birds. *Condor*, **54**, 121-136.

Dunnet, G. E. & Hinde, R. A. (1957). Chapter on other passerine species in *U.F.A.W. Handbook on the Care of Laboratory Animals*. London, U.F.A.W.

Ficken, R. W., van Tienhoven, A. von, Ficken, M. S. & Sibley, F. C. (1960). Effect of visual and social stimuli on breeding in the budgerigar. *Anim. Behav.*, **8**, 104-107.

Hinde, R. A. (1958). The nest-building of domesticated canaries. *Proc. zool. Soc. Lond.*, **131**, 1-48.

Hinde, R. A. & Warren, Roslyn, P. (1959). The effect of nest-building on later reproductive behaviour in domesticated canaries. *Anim. Behav.*, **7**, 35-41.

Lehrman, D. S. (1959). Hormonal responses to external stimuli in birds. *Ibis*, **101**, 478-496.

Marshall, A. J. (1959). Internal and environmental control of breeding. *Ibis*, **101**, 456-478.

Rowan, W. (1931). *The Riddle of Migration*. Baltimore.

Vaugien, L. (1951). Ponte induite chez la Perruche ondulée maintenue à l'obscurité et dans l'ambience des volières. *C. R. Acad. Sci.*, Paris, **232**, 1706-1708.

Warren, Roslyn P. & Hinde, R. A. (1959). The effect of oestrogen and progesterone on the nest-building of domesticated canaries. *Anim. Behav.*, **7**, 209-213.

Accepted for publication 14*th September*, 1960.

SOCIAL FACILITATION IN GREEN TURTLE SIBLINGS*

By ARCHIE CARR and HAROLD HIRTH

Department of Biology, University of Florida, Gainesville, Florida

Introduction

During her biennial or triennial trip to the nesting beach the green turtle (*Chelonia mydas*) lays between 500 and 1,000 eggs, parcelled out at 12-15 day intervals in clutches of about 100. The waters around rookeries are usually deep, rough, and foodless, and one wonders why the turtle should not nest a single time and leave for home pastures. Perhaps the 100-egg complement is the fraction that gives just the right spreading of risk of nest predation. Also, it is unlikely that the capacity to carry 1,000 shelled eggs to the beach at one time could be evolved, while to reduce either the number or the size of the eggs would affect the reproductive potential. Even if the full load could somehow be carried ashore there would be too much volume to be lodged in the zone of stable microclimate: below about a foot, and above the level of waterlogged sand. Moreover, 100 eggs just fill the flask-shaped nest the turtle makes. If the shape is functional, as seems likely, then nest-shape alone would hold down egg number, because the leg and foot of the turtle are extended to the limit in digging the 100-egg nest. Other factors no doubt help regulate the upper limit of complement size. We are here interested in those that keep it from falling below a certain minimum, and social facilitation seems to be involved.

Mechanical and Psychological Co-operation

Carr & Ogren (1959) suggested that a single sea turtle, hatching at the usual nest depth, would be unlikely to survive. Tests made at Tortuguero, Costa Rica, during July, 1959, support this assumption. Results are shown in Table I. Figures in the table refer only to hatchlings reaching the surface of the sand. In a few of the tests observations were continued after emergence, and these tend to strengthen the case for group facilitation. Of the six single hatchlings that got to the surface, none came out, in the opinion of the observer, able (or motivated) to crawl to the sea. Two were even unable to cross the few feet of sand to the wire fence that surrounded the experimental nests. In the larger groups kept under observation, however (two sets of five, one of nine, two of ten) all the emerging young actively moved to the seaward side of the enclosure and piled up there. Tests to determine the bearing of this post-emergence behaviour on survival are projected. Meantime, however, it seems clear that some sort of social advantage is involved, and it is of interest to examine the factors that may contribute toward it.

Table I. Relation between Brood-size and Emergence-success in Green Turtle Nests at Tortuguero, Costa Rica, June-September, 1959. All hatchlings were from divided egg complements re-buried at depths of 30-34 inches. The rank correlation between the number of hatchlings per nest and the percentage survival is 0·092, which is significant at the 0·05 per cent. level.

No. live turtles hatched in the nest	No. of nests	No. of hatchlings emerging	Percentage emergence
1	22	6	27·3
2	22	37	84·1
3	18	49	90·7
4	14	55	98·2
5	13	64	98·5
6	12	71	98·6
7	12	82	97·6
8	13	104	100·0
9	6	54	100·0
10	4	40	100·0

Observations through glass nest-sides (Carr & Ogren, 1959, 1960, and unpublished data) support the implication of the above data that turtles in a nest are not independent individuals but a group that meets the shared predicament of its interrment with group action. The first young that hatch do not start digging at once but lie still until some nestmates are free of the egg. Each new hatching adds to the working space, because the spherical eggs and the spaces between them make a volume greater than that of the young and the crumpled shells. The vertical displacement that will carry the turtles to the surface is the upward migration of this chamber, brought about by a witless collaboration that is really a loose sort of division of labour. Although the movements involved are only a generalized thrashing, similar to those

*This work was supported by a grant from the National Science Foundation (G-10717).

that free the hatchling from the egg, they accomplish four different (and perhaps indispensable) things, depending on the position of the turtle in the mass. Turtles of the top layer scratch down the ceiling. Those around the sides undercut the walls. Those on the bottom have two roles, one mechanical and the other psychological: they trample and compact the sand that filters down from above, and they serve as a receptor-motor device for the hatchling superorganism, stirring it out of recurrent spells of lassitude. Lying passively for a time under the weight of its fellows one of them will suddenly burst into a spasm of squirming that triggers a new pandemic of work in the mass. Thus, by fits and starts, the ceiling falls, the floor rises, and the roomful of collaborating hatchlings is carried toward the surface.

Once the young turtles are on the beach, whatever integration remains is maintained by the common motivation and taxes that take the hatchlings toward the sea. Although co-operative advantage at this stage remains to be shown experimentally, observations suggest that some interchange continues. The trip to the sea is interrupted repeatedly. This may prolong the period of exposure to desiccation and predation. A broodmate coming up from behind often stimulates a stalled group to move off abruptly, like toy turtles wound up and all let go together. Moreover, when one of a generally well-oriented group collides with a fellow off its course they both are likely to resume the journey on correct headings after the collision. Once in the water, the sibling group is so spread about by the trip through the surf that facilitation may be of little importance. Watching groups of hatchlings that have crossed the surf line to the calmer water beyond, we have occasionally seen one take a swimming cue from another; but this must be a minor effect with little bearing on survival.

Heat Gain in Green Turtle Nests

The figures in Table I represent survival of hatched-out turtles—not survivors from egg clutches. Moorhouse (1933) found reduced viability in fractional complements of eggs placed in artificial nests, and attributed this to injury in transportation. Hendrickson (1958) thought it more likely caused by lowered metabolic heating in the small egg masses, having found that, during a two-week period at the China Sea rookeries, nest temperatures gained an average of 5·9 degrees Centigrade over the outside average at the same depths. Our data comparing temperatures inside and outside the nests at Ascension Island (Fig. 1) show an average gain of 2·3 degrees Centigrade in nests.

While it is possible that some of the rise in temperature is the result of decomposition of infertile or defective eggs, the character of the degeneration that these undergo—gradual shriv-

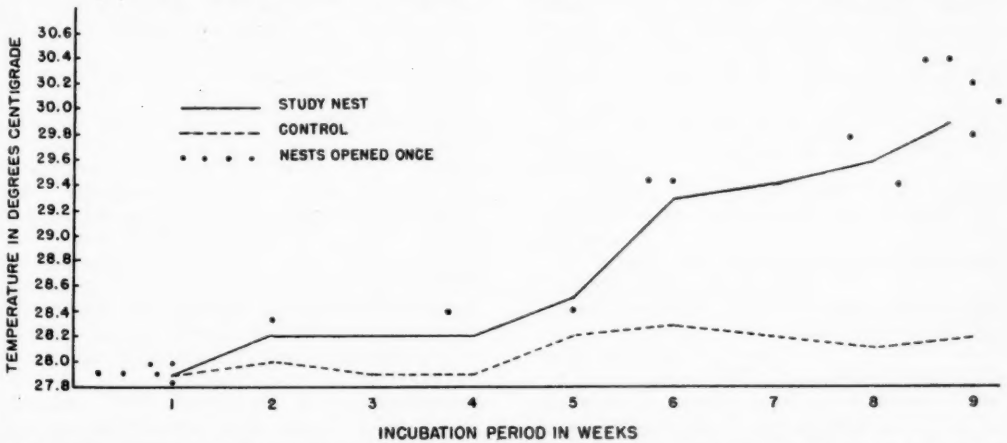


Fig. 1. Temperatures in turtle nests and outside at the same depth (about 31 inches); Ascension Island, 23rd Feb.—24th April, 1960. Temperatures for the study nest and control were taken four times daily at the bottom of a tube inserted into the nest, and are given as weekly averages. Diel ranges were 1 degree Centigrade or less. From the 105 eggs in the study nest, laid by a turtle with carapace length of 43 inches, 63 young emerged after 61 days' incubation. The rest were infertile or produced dead or deformed embryos.

elling and solidification—make this factor seem less probably significant than the mass metabolizing of the live eggs. If the self-heating actually influences viability and hatching time, which remains to be shown, it might explain some of the incongruence between our small high survival groups (Table I) and the oddly large safety factor the female seems to be allowing when she stocks a nest with 100 eggs.

Summary

1. Tests made at the green turtle nesting ground at Tortuguero, Costa Rica, show that turtles hatching singly have reduced prospects of emerging from the nest, and even less chance of reaching the sea.

2. Observations through glass nest sides, and of young going from the nest to the sea, show that group facilitation, probably involving both mechanical and psychological factors, occurs.

3. Data from tests at Ascension Island, extending Hendrickson's results (1958) in the China Sea, indicate that metabolic heating raises the temperature in nests of developing green turtle eggs and suggests that this may constitute thermal co-operation affecting the fitness of the sets of eggs and young as evolutionary units.

REFERENCES

Carr, Archie & Larry, Ogren (1959). The ecology and migrations of sea turtles. 3. *Dermochelys* in Costa Rica. *Amer. Mus. Novit.*, 1958, 1-29, 13 figs.

Carr, Archie & Larry, Ogren (1960). The ecology and migrations of sea turtles. 4. The green turtle in the Caribbean Sea. *Bull. Amer. Mus.*, **121** (1), 1-48.

Hendrickson, John R. (1958). The green sea turtle, *Chelonia mydas* (Linn.), in Malaya and Sarawak. *Proc. zool. Soc., Lond.*, **130** (4), 455-535.

Moorhouse, F. W. (1937). Notes on the green turtle (*Chelonia mydas*). *Rept. Great Barrier Reef Comm.*, **4**, 1-22.

Accepted for publication 31*st August*, 1960)

HIERARCHICAL BEHAVIOUR IN THE SOUTH AFRICAN CLAWED FROG *Xenopus laevis* Daudin*

By ROBERT HAUBRICH

Science Department, East Carolina College, Greenville, North Carolina

Introduction

The observations reported here were designed to identify any forms of aggressive behaviour in *Xenopus*, and to determine whether aggression, if it exists, produces a type of hierarchical behaviour. Recent works have reported instances of aggression and territoriality in the Class Amphibia. Martof (1953) described a type of territoriality among breeding males of the green frog, *Rana clamitans*. Pearson (1955) observed avoidance reactions and a type of undefended home site territory in the spadefoot toad, *Scaphiopus holbrooki holbrooki*. Test (1954) reported definite evidence of aggression in the frog *Phylobates trinitatis* in defence of territory. Goin (1955) indicated further evidence of territoriality based upon aggression for the bullfrog, *Rana catesbeiana*. Grant (1955) reported territoriality in two species of salamanders, *Eurycea bislineata* and *Hemidactylium scutatum*. The means of defence involved a direct biting attack in the former and challenging in the latter.

Methods

Xenopus laevis, first described by Daudin (1803), is primarily an aquatic frog. However, at times the animal moves overland or lives in clods of mud near dried-up ponds (Leslie, 1890; Rose, 1950). The animals in this study were all females and were obtained as adults from South Africa via the supply house of J. E. Cook, Cockeysville, Maryland (Walker, 1952). Before each experiment, groups of four animals were kept in five-gallon aquaria containing ten inches of water protected from direct sunlight and at temperatures between 60° and 75°F. As suggested by Parker, Robbins & Loveridge (1947), the water was changed after each feeding or when it became cloudy. Experiment I was conducted in the Marine Biological Laboratory at Woods Hole, Massachusetts, from June to August, 1954. Experiment II was conducted during the summer and fall of 1955 at the University of Florida, Gainesville.

*This paper represents a dissertation presented to the Graduate School of the University of Florida in August, 1957.

Experiment I

Twelve frogs (two groups of six) were kept in two ten-gallon aquaria between observations and were weighed once a week during the experiment al period. Certain digits on the front limbs were clipped to facilitate recognition and even though the digits regenerated, size, colour pattern, behaviour and body shape varied sufficiently to permit recognition.

The animals were observed in pairs in a five-gallon aquarium. Cubes of liver, about ¼ inch on a side, were placed in the aquarium one at a time as the animals ate them. Food was offered only during times of observation and the number of units eaten by each frog was recorded.

Each pair was observed in two sets of five consecutive twenty-minute periods in any one set to prevent fatigue in the observer. After each series of five periods the pair under observation was removed and placed in one of the storage aquaria with other frogs. The water was then changed in the observation tank and another pair of frogs was selected for observation. Pairs were chosen by a round robin type of selection which permitted at least five consecutive twenty-minute periods for a pair following the pattern described above. Each pair, therefore, was observed a total of 200 minutes divided into two sets of five twenty-minute periods.

Each time animals made contact, one of the following units of behaviour was recorded for each frog:

1. *Nipping*. One frog nipped or bit another and caused its retreat with no damage perceptable.
2. *Pushing*. One frog approached another and displaced it through contact.
3. *Approaching*. An individual approached and made contact with its pair-mate which did not move away as a result.
4. *Unclassified*. When two animals made contact while in motion with no observable differential between them, the activity was recorded as unclassified because the observer could not interpret the behaviour.

Observations were also conducted with isolated animals in which the timing procedure

duplicated that of the paired situation. The following information was recorded for each frog while isolated:

1. Number of cubes of liver eaten.
2. Time in seconds taken to obtain each piece of liver. Attempts were made to be consistent in placing liver in the aquarium as far away from the frog as possible and out of the direct line of vision.

Experiment II

Frogs were kept isolated at all times between observations in one-gallon jars in order to prevent a possible carryover of behaviour from any grouped situation. Paired and isolated animals were observed as in Experiment I. The temperature varied between 71°—74°F. An additional series of observations in Experiment II were made on each animal as a member of a group of twelve to determine whether position in any hierarchy would be consistent under different conditions. Since it was impossible to record the activities of all frogs in the aquarium simultaneously, the behaviour of each frog with reference to the other eleven was observed separately for a total of 200 minutes. Because of intense activity no record was kept of which animals nipped or received nips from the frog under observation. Experimental procedure was similar to that used in the paired situation, except the animals were isolated a minimum of twelve instead of twenty-four hours after each daily observation.

Results

Rankings of animals in nips, pushes or approaches given were obtained from totals along the bottom rows of charts as indicated for nips only in Table I. Rankings of animals in nips, pushes and approaches received were obtained from totals along the right column of charts as indicated below for nips. For example, in Table I, frog one nipped frog four nineteen times as shown by the first figure in column one. Frog one, however, received seventeen nips from frog four as indicated at the top of column two. The total, 279, at the bottom of column one, indicates the number of nips given out by frog one, while the total, 76, at the right end of row one indicates the number of nips received by frog one. The asterisks indicate a significant difference in number of nips given as compared to nips received for any particular pairing. For example, the third number in column one, which is 25, has an asterisk after it. This indicates frog one nipped frog six twenty-five times, while frog six nipped frog one ten times, as seen at the top of column four. The difference between these values was found to be significant at the five per cent. level when tested by means of the t-test.

$$t=\frac{\bar{\Delta}}{SE_{\bar{\Delta}}} \text{ in which:}$$

$$\bar{\Delta}=\frac{\Sigma\Delta}{n}=\text{Average difference}$$

$$SE_{\bar{\Delta}}=\sqrt{\frac{\Sigma\Delta^2-\Delta(\Sigma\Delta)}{n(n-1)}}=\text{Standard error of mean differences}$$

The various rankings and correlations concerned with food consumption were obtained from charts similar to Table I.

Table I. Total Nips Given by Frogs in Pair Combinations. Experiment I

Frog no.	1	4	2	6	5	12	11	7	10	9	8	3	Total
1	..	17	14	10	5	5	4	5	5	4	4	3	76
4	19	..	12	9	9	5	6	6	3	3	2	2	76
2	16	10	..	20	5	3	4	5	5	8	5	5	86
6	25*	12	17	..	9	11	9	5	3	7	8	1	107
5	10	20	12	10	..	9	4	7	3	6	1	9	91
12	41*	15*	7	9	18	..	10	7	9	3	1	1	121
11	23*	16*	10	8	7	8	..	9	7	2	7	2	99
7	16*	22*	18*	21*	15	6	9	..	10	6	7	8	138
10	29*	13*	13	18	15	14	8	17	..	4	9	3	143
9	26*	19	17	16	21*	21*	22	25	11	..	7	5	170
8	37*	45*	18	28*	18*	27*	21*	26*	12	13	..	9	254
3	37*	32*	35*	22*	5	11*	15*	11	11*	10	2	..	191
Total	279	221	173	171	127	120	112	103	79	66	53	48	1552

*A significant difference in number of nips given for any particular pairing is indicated by an asterisk following the greater value. For further explanations see discussion above.

Table II.* Rank Correlations Between Nips, Pushes or Approaches Given and Nips, Pushes or Approaches Received.

Experiment number	Behavioural category	Rank correlation	P<
I	Nips given/Nips received	—0·96	0·01
II	" " " "	—0·50	·1
I	Pushes given/Pushes received	—0·87	·01
II	" " " "	—0·76	·01
I	Approaches given/Approaches received	—0·83	·01
II	" " " "	—0·88	·01
	Rank correlations from food consumption charts		
I	Bottom row/Right column	—0·82	·01
II	" " " "	—0·48	·1

*The rank correlations observed above were obtained by use of the following:

$\acute{\eta}=\frac{1-6\Sigma(d^2)}{m^3-m}$ in which: $\acute{\eta}$=rank correlation
d=difference between rankings
m=number of animals

The correlations were tested for significance by use of the following modified t-test:

$t=\frac{\acute{\eta}}{\sqrt{1-\acute{\eta}^2}}\sqrt{m-2}$ in which: $\acute{\eta}$=rank correlation
m=number of animals

Table III. Total Units of Food Eaten by Frogs During Observation Time of 200 Minutes when Isolated, Paired* and in Group of Twelve. Experiment II.

Frog number	Total units eaten		
	Isolated	Paired*	Grouped
101	56	32	106
102	50	73	167
103	113	68	157
104	0	36	191
105	55	39	81
106	50	31	98
107	69	64	110
108	0	62	19
109	25	28	41
110	5	12	21
111	12	7	68
112	6	32	140
Total**	441	484*	1199

*Average value of 200 minutes taken from total observation time of 2400 minutes for each frog.
**The three totals were tested for statistical significance by means of the t-test (see Table I) with the following results:

Isolated/Grouped, P< ·01
Isolated/Paired, P> ·05
Paired/Grouped, P< ·05

Discussion

The nip, push and approach categories appear to represent expressions of aggression in this animal and individual variations within each of these categories resemble hierarchies found in other vertebrates. There is an inverse relation in most cases between nips, pushes or approaches given and nips, pushes or approaches received (see Tables II and IV). These findings are consistent whether frogs are observed in series of pairings or in a group of twelve. However, no matter how great the aggressive differential is between any two animals, usually the subordinate member reciprocates with some aggressive actions (Table I). In hens which display nip-right behaviour, the side of any chart representing activity of subordinate animals contains mostly zeros excepting occasional large numbers indicating a hierarchial triangle (Banks, 1956). In cattle a similar picture is presented by Schein & Fohrman (1955) and certain fishes such as *Platypoecilus maculatus* also demonstrate this condition (Braddock, 1949). The latter situations picture very positive expressions of hierarchial behaviour while the situation observed with the frogs is a much less obvious expression of individual aggressive differences.

There is no evidence of any releasing order in these levels of aggression similar to those reported by Braddock (1955) for the Siamese fighting fish. However, an inverse relation exists between frequency and relative intensity of aggression which is consistent with findings in

Table IV.* Rank Correlations of the Categories with Tests Indicating Probability of Correlation being as Large or Larger Due to Chance Alone (Edwards, 1954).

Comparisons	Frogs 1-12		Frogs 101-112	
	Correlation	P<	Correlation	P<
Nip/Push	0·85	0·01	0·81	0·01
Nip/Approach	·94	·01	·70	·01
Push/Approach	·84	·01	·94	·01
Nip/Unclassified	·40	·2	·61	·05
Push/Unclassified	·32	·3	·77	·01
Approach/Unclassified	·35	·3	·85	·01
Paired Gruuped				
Nip Nip	....	....	·81	·01
Push Push	....	....	·71	·01
Nip Push	....	....	·76	·01
Grouped Nip/Grouped Push	....	....	·97	·01
Nip/Food eaten	·66	·02	·85	·01
Push/Food eaten	·55	·1	·90	·01
Approach/Food eaten	·64	·05	·87	·01
Unclassified/Food eaten	·56	·1	·76	·01
Nip/Food time	·82	·01	·27	·4
Push/Food time	·55	·1	·36	·3
Approach/Food time	·64	·05	·36	·3
Unclassified/Food time	·52	·1	·06	·9
Nip/Weight	·52	·1	·91	·01
Push/Weight	·67	·02	·80	·01
Aproach/Weight	·49	·1	·80	·01
Unclassified/Weight	·08	·8	·63	·05
Food eaten/Food time	·73	·01	·26	·5
Food eaten/Weight	·10	·8	·70	·01
Food time/Weight	·38	·3	·28	·5

*Statistical methods used in Table IV are similar to those discussed at the bottom of Table II.

other vertebrates (Denenberg, 1959). Contacts of the unclassified type constitute over 60 per cent. of all contacts while slightly more than 20 per cent. are represented by the approach, about 7 per cent. by the push and 5 per cent. by the nip. A greater frequency of pushing as compared to nipping is also seen when frogs are assembled in a group of twelve.

Heavier frogs tend to rank higher in the three aggressive categories, yet do not necessarily rank higher in the unclassified category (Table IV). This situation agrees with findings in other hierarchial studies (Schein & Fohrman, 1955) which indicate both size and age often, but not universally, are factors in expression of relative aggressive differential.

Differences in food consumption are not as clear-cut as those within each of the aggressive categories. Somewhat less than 50 per cent. of the pairings show significant differences between frogs, and when rankings of frogs in total food consumed are compared to rankings in total food consumed by others in their presence all correlations are negative but not all significantly (Table II).

Differences in average time taken to locate food may be due to variations in the chemoreceptor systems and in ability to respond to these stimuli. The more aggressive frogs do not necessarily find food more quickly, nor do the frogs eating more while paired necessarily take the least time to locate food when isolated so (Table IV).

Aggression in *Xenopus* appears to be linked to eating behaviour. Cannibalism is well known in this species (Rose, 1950) and the behaviour preceding nipping is observed to be nearly identical to that leading to the consumption of liver or earthworms. Often as nips were delivered, only the size and movement of the pair-

mate seemed to prevent its being eaten, and in one case one animal partially swallowed the foot of another. An increase in the frequency of nipping, pushing and approaching in the presence of food is further evidence supporting this assumption. The total amount of food consumed varied directly with the number of animals placed together (Table III). The chances of food being found were enhanced when more animals occupied a certain volume of water, but other factors apparently contributed to this result. A short time after a unit of food was placed in an aquarium with a group of frogs, the frequency of sweeping motions with the front feet and the amount of swimming activity both increased as did frequencies of all types of contacts. Even after the food had been eaten, the increased activity continued for 10-30 minutes. Also, a type of behaviour that suggested searching by one or two frogs in a group initiated the same sort of activity among the others even in the absence of food.

Correlations are generally higher in Experiment II than in Experiment I (Table IV). It is probable that the experimenter learned to interpret the behavioural elements with more accuracy and improved technique as the observations went on. Also, animals in the second group were isolated between observations. The differences between the two sets of correlations also undoubtedly reflect basic differences between the two groups of frogs. Although no direct evidence is available on age, it is assumed that the average age of the second group was considerably younger than that of the first group. This evidence comes from a comparison of average weight (Frogs 1-12—90·5 grammes; Frogs 101-112—76·17 grammes) and from general activity and condition of the animals.

Aggression and hierarchial behaviour in *Xenopus* show the following characteristics that permit comparisons with other behavioural studies:

1. No absolute displays of dominance of one individual over another are seen, although significant differences do occur frequently.

2. Individual recognition, while suggested, is not obvious.

3. No form of challenge is visible.

4. The behaviour pattern of aggression is similar to eating behaviour.

5. While three distinct types or levels of aggression are apparent, no releasing order is evident.

Summary

Aggression in *Xenopus* is expressed behaviourally by the approach, the push and the nip which represent increasing intensities of aggression in the order given. There is an inverse relation between intensity of the aggression and frequency of occurrence. A category designated as "unclassified" represents contacts in which no aggression is visible, and the total frequency of such contacts is as great or greater than all other types combined. Heavier frogs display aggressive behaviour more frequently than do lighter ones and more aggressive frogs eat more than less aggressive animals. Individuals eat least when isolated, more when placed with one other frog and most when placed with eleven others. Differences between the isolated and paired situations are not significant, but total individual consumption in groups is significantly greater than either the isolated or paired conditions.

Acknowledgments

I am deeply indebted to the late Dr. W. C. Allee of the University of Florida for supervision, aid and inspiration during the early days of this work.

Dr. E. Ruffin Jones of the University of Florida deserves many thanks for supervision, suggestions and critical reading of the manuscript after the death of Dr. Allee.

I am indebted to Dr. James C. Braddock of Michigan State University for critical reading of the manuscript.

REFERENCES

Banks, E. M. (1956). Social organization in red jungle fowl hens (*Gallus gallus*). *Ecology*, **37**, 239-248.

Braddock, J. C. (1949). The effects of prior residence upon dominance in the fish, *Platypoecilus maculatus*. *Physiol. Zool.*, **22**, 161-169.

Braddock, J. C. & Braddock, Z. I. (1955). Aggressive behaviour among females of the Siamese fighting fish, *Betta splendens*. *Physiol. Zool.*, **28**, 152-172.

Daudin, F. M. (1803). *Histoire naturelle des Rainettes, des Grenouilles et des Crapauds*. Paris. p. 85.

Denenberg, V. H. & Bell, R. W. (1959). Relationships between social relations and avoidance conditioning. *Physiol. Zool.*, **32**, 51-56.

Edwards, A. L. (1954). *Statistical methods for the behavioral sciences*. New York: Rhinehart & Company, Inc., 542 pp.

Goin, O. B. (1955). *World outside my door*. New York: MacMillan Co. p. 43.

Grant, W. C. (1955). Territorialism in two species of salamanders. *Science*, **121**, 137.

Leslie, J. M. (1890). Notes on the habits and oviposition of *Xenopus laevis*. *Proc. zool. Soc., Lond.*, 69-71.

Martof, B. S. (1953). Territoriality in the green frog, *Rana clamitans*. *Ecology*, **34**, 156-174.

Parker, F., Jr., Robbins, S. L. & Loveridge, A. (1947). Breeding, rearing and care of the South African Clawed Frog (*Xenopus laevis*). *Amer. Nat.*, **81**, 38-49.

Pearson, P. G. (1955). Population ecology of the spadefoot toad, *Scaphiopus h. holbrooki* (Harlan). *Ecol. Monog.*, **25**, 233-267.

Rose, W. (1950). *The reptiles and amphibians of Southern Africa.* Cape Town: Maskew Miller Ltd. pp. 1-34.

Schein, M. W. & Fohrman, M. H. (1955). Social dominance relationships in a herd of dairy cattle. *Brit. anim. Behav.*, **3**, 45-55.

Test, F. H. (1954). Social aggressiveness in an amphibian. *Science*, **120**, 140.

Walker, C. (1952). Clawed toad capital of America. *The Sunday Sun Metrogravure.* Baltimore, Md., April 30.

Accepted for publication 31*st August*, 1960.

SPACING PATTERNS OF FEMALE *Drosophila paramelanica*

By OWEN J. SEXTON and HARRISON D. STALKER
Washington University, St. Louis, Missouri

Individuals or social groups of many species of vertebrates, from teleosts to mammals, maintain some sort of spatial distribution in which the individual or social group occupies a specific area to the exclusion of other individual or social groups of that same species. The defence of such an area, termed the territory, may be made by animals of one or of both sexes, and the resident defends the territory either through a series of overt acts which do not culminate in physical contact between the resident and the trespassing non-resident or by actual physical contact.

The comparable situation among the invertebrates has been less extensively studied, but it is known that certain insects do exhibit territorial defence while others disperse themselves to the extent that the individuals of a population are fairly evenly distributed. Jacobs (1955) has provided a short review of territoriality among dragonflies and has reported on detailed studies of territorial behaviour in two particular species. The occurrence of social dominance and territoriality among crickets has been indicated by Alexander (1959). Naylor (1959) investigated the spatial distribution of male and female *Tribolium confusum* in unisexual and bisexual populations and found that there is a tendency for these beetles to space themselves uniformly under certain conditions. Free (1958) observed that bumble bees defended their colony against the intrusion of bees from other colonies.

Casual examination of *Drosophila paramelanica* raised in standard laboratory culture bottles and vials indicated the possibility that these flies arranged themselves uniformly over the substrate rather than randomly or in aggregations. Clark & Evans (1954) have provided a technique yielding a quantitative value, termed R, which indicates whether or not the members of a population are aggregated, randomly distributed, or evenly spaced. The value $R = \bar{r}_A / \bar{r}_E$ where $\bar{r}_A$ is the observed mean distance between nearest neighbours in a population and where $\bar{r}_E$ is the mean distance between nearest neighbours expected in a randomly distributed population of the same density. The R value may vary from a low of 0·0 which indicates that the individuals within the population exhibit extreme clumping or aggregation through 1·0 which indicates that the individuals are randomly distributed to a maximum of 2·1491, which indicates that the organisms are as evenly distributed as is possible. The present investigation is a study of the spacing patterns of *D. paramelanica* at different population levels.

Methods

The Flies

The *D. paramelanica* used were all F_1 female progeny from experimental crosses and were phenotypically wild type. They were reared under uncrowded conditions on a standard corn meal agar medium enriched with live yeast. The newly emerged flies were separated from their brothers during the first two days of adult life and were allowed to mature for 6-10 days on the standard medium before they were used in the experiments. The flies were raised at 25°C.

The Apparatus (Plate II)

The R values were determined for populations of females which had alighted on the exposed lower surface of a piece of moist filter paper. Hence, the flies were hanging suspended from that lower surface. The upper surface of the filter paper was adherent to a piece of translucent circular Plexiglass fitted into the lower end of a hollow brass piston. The upper end of the piston was open. The piston itself was movable and fitted down into a cylindrical chamber within a block of black Plexiglass. The block was 10·2 cm. deep and 7·5 cm. along each side. The cylindrical chamber within the black Plexiglass block had a diameter of 6·3 cm. and the effective depth of the chamber could be varied by moving the piston up or down. The lower end of the cylindrical chamber, opposite to that in which the piston was inserted, was covered with an immovable piece of transparent glass. The flies were introduced into the chamber by means of a passageway of 25 mm. diameter through the wall of the block. This smaller chamber could be readily plugged so that the flies could not escape.

A 100-watt light bulb was located beneath the apparatus, and a flash light minus its reflector was placed above it. The flashlight could be swung out of position readily. Either light source could illuminate the interior of the

cylindrical chamber. A 35 mm. camera was placed above the flashlight and was used to take pictures through the hollow brass positon of the flies suspended from the moist filter paper.

Photographing the Flies

After a number of flies were introduced into the cylindrical chamber within the black Plexiglass block, they tended to become concentrated on the moist filter paper covering the top of that chamber. The lower light source was then turned on, and the camera was focussed on the flies on the filter paper. Next, the lower light was switched off, and the flash-light swung into position over the open end of the hollow brass piston and switched on, The apparatus remained in this condition for several minutes. Then the flash light was quickly moved out of position, the lower light turned on, and the camera shutter was released. The flies hanging suspended from the filter paper were photographed in the positions they had assumed on the paper.

The number of flies on the filter paper could be varied by introducing more flies into the chamber or by decreasing the volume of the chamber and increasing the density of the flies.

Mapping the Position of the Flies

The finished negative was placed in a projector, and the image projected onto a vertical piece of white paper. The outline of the circular filter paper was traced on the white paper, and the position of each fly was indicated by placing a dot on the paper at the mid-thorax. Next a smaller circle having a diameter of 3·14 cm. and concentric with the outline of the filter paper was drawn. The area of this circle was 2066 mm.^{2} The dots within this smaller circle were used to determine the observed distances between nearest neighbours and to determine the density of the flies.

Results

Importance of Non-biological Factors in Affecting the Distribution of the Flies

In order to determine the relationship between population levels and spacing patterns, it is necessary to eliminate extraneous factors, such as light, which also might produce changes in spacing patterns. If the flies responded differentially to areal variations of such factors, one would expect to find the individual flies aggregated in some areas and absent in others. Two separate series of chi-square tests have indicated that the flies were not clumped but were uniformly distributed over the lower surface of the filter paper.

Four populations were used in the first test. In each instance the circle on the filter paper within which the flies were distributed was divided into a central circle and three concentric rings. The area of each of these four figures was one quarter of the area of the original, large circle. Hence, if the flies were responding to some physical factor which varies in intensity radially, one would expect that they would not be equally distributed amng the four concentric figures. The observed and expected frequencies of the flies present in each of the four figures was determined and then compared by use of a chi-square test. None of the four chi-square values, 0·47, 5·05, 1·98, and 4·45, all with 3 degrees of freedom, indicated a significant departure from randomness.

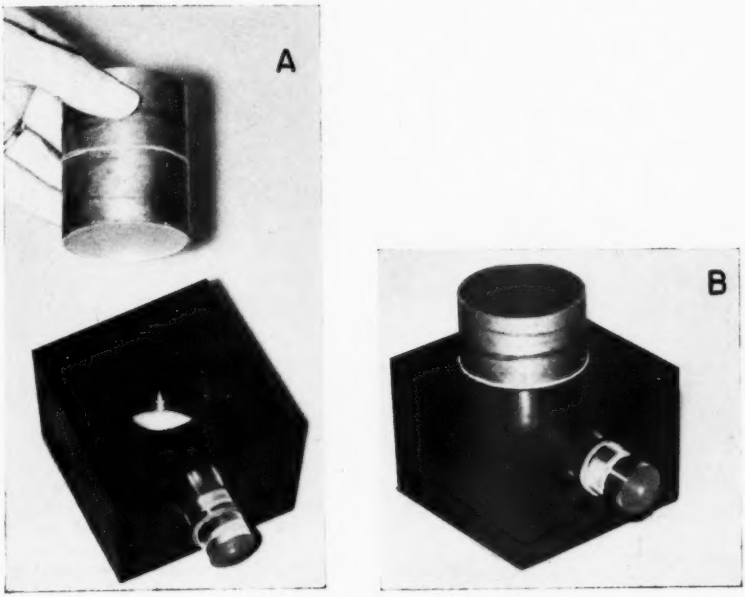
Four different populations were examined in the second test. The circle on the filter paper within which the flies were distributed was divided into four equal quadrats, each quadrat having one quarter of the area of the circle. If the flies were responding to a factor which varied in intensity from the right to the left of the circle, or from the top to the bottom of the circle, one would expect that the flies would not be distributed equally among the four quadrats. Again the observed and expected frequencies of the flies in each of the quadrats was determined and compared by use of the chi-square test. In no case was the distribution of the flies among the four quadrats significantly different from expectation. The chi-square values were 0·02, 0·33, 1·17, and 1·29, all with 3 degrees of freedom.

On the basis of these two series of tests, it can be concluded that physical factors did not vary in such a fashion as to affect the spacing patterns of the flies.

The Spacing Patterns of the Flies

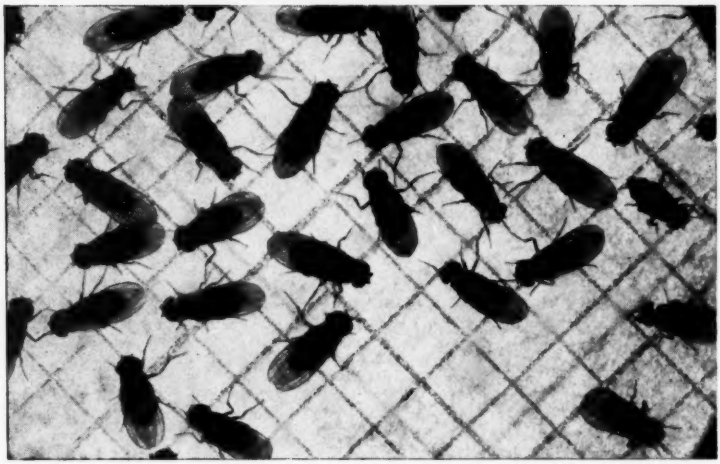
The R values for 36 populations of flies were determined, and these values ranged from a low of 1·15 for a population of 35 flies to a high of 1·60 for a population of 183 individuals. Only one of the R values, 1·15, did not differ significantly from the R value of 1·0 expected for populations distributed at random. All of the other 35 R values differed significantly, at the 5 per cent. level or better, from the values expected for a population of flies distributed at random, clearly indicating that the females of

PLATE II



The basic part of the apparatus used to measure the spacing patterns. The flies were contained within the cylindrical chamber of the block of black Plexiglass shown in A. The lower end of this chamber was closed by a fixed piece of glass. A hollow brass cylinder fitted into the upper end of the chamber as in B. This cylinder was movable. Flies were introduced into the chamber through a small hole which could be plugged with a solid Plexiglass cylinder, figured in both A and B. The flies which were photographed were those which had alighted on a piece of moist filter paper adherent to the ground Plexiglass gase of the brass cylinder. The Plexiglass base is shown in A.

PLATE III



Females of *Drosophila paramelanica* suspended from a surface. Some of the females have extended their legs as if to ward off adjacent animals. This photograph was not taken under the standard conditions used in the experiments. The hazy areas are flies on a lower transparent surface.

D. paramelanica are distributed at fairly regular intervals over the surface of the filter paper.

There appears to be a positive correlation between the size of the R value and the size of the populations when the latter are between certain levels (Fig. 1). In the population size range of 21 to 70 individuals, the R value varied from a low of 1·15 to a high of 1·51. The

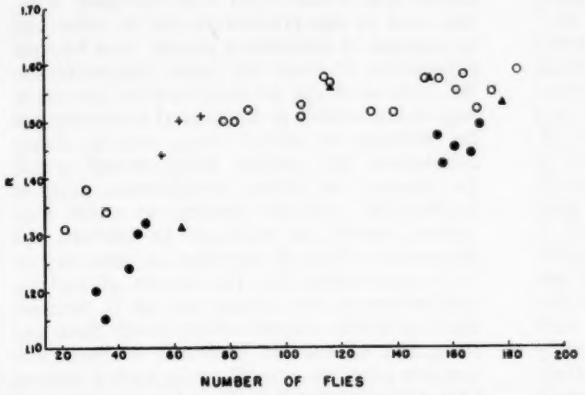


Fig. 1. The graphical relationship between population size and R values. The number of flies on the abscissa refers to the number of flies occupying the 2066 mm.^{2} of filter paper surface. Only one R value, 1·15, did not differ significantly from 1·00, the value expected for populations distributed at random. The various symbols represent groups of flies measured on different days as follows: solid triangle, May 24th, 1959; solid circle, July 19th, 1959; open circle, Sept. 26th, 1959; plus sign, Jan., 2nd, 1960.

coefficient of correlation, r, for population size and R values is 0·612 which is significantly different at the 5 per cent. level from r=0·0. This positive correlation indicates that the flies become more uniformly spaced as the population increased from 21 to 70 flies. Presumably, this same relationship holds at lower population levels also so that the R value would increase from 1·0 at very low population levels to 1·5 at levels of 70 flies per population.

In contrast with this increase in R value as the population size increases from 21 to 70 individuals is the relative constancy of the R value for those populations consisting of between 80 and 183 flies. At these latter population levels the R values fluctuate about a mean of 1·53, indicating that the spacing pattern of the flies has become relatively stabilized, although there may well be a gradual increase in R value.

The greatest number of flies ever observed on the 2066 mm.^{2} circle on the filter paper was 183 in spite of the fact that as many as 1,000 flies were introduced into the cylindrical chamber. The remainder of the flies were on the walls of the chamber or piled up on the bottom. At populations of 50 flies, at least 90 per cent. of the flies are located on either the upper or lower surfaces of the cylindrical chamber, indicating that these surfaces are more frequently occupied than are the walls. This limitation in the number of flies on the upper surface as well as the high R values indicate that the flies are exerting some sort of control over the occupancy of the areas adjacent to them.

Discussion

At the lowest population levels observed at which the R value differed significantly from 1·0, 21 flies occupied the 2066 mm.^{2} of the filter paper surface. Thus, there were 98·3 mm.^{2} of filter paper surface per fly. At the population level at which the R value became relatively stabilized, 80 flies were on the paper so that there were 25·8 mm.^{2} of surface per fly. Finally, at the highest population levels observed, there were 183 flies, and 11·3 mm.^{2} of surface per fly. In all three cases an individual fly occupied an area greater than the 9·3 mm.^{2} of the filter paper surface which was actually covered by the body, wings, and legs of a fly as it hung suspended from the filter paper.

These data suggest that each fly exerts some control over the areas adjacent to it, but this apparent domination should not be construed as being evidence for territoriality. Observations of living flies moving about over both the upper and lower surfaces of the cylindrical chamber in the experimental apparatus clearly indicate that flies do not actively rush towards an intruding fly in order to defend a certain area. Thirty-five contacts between pairs of flies, one of which was walking while the other was not, were observed. In 25 of the cases the walking fly was seen to approach the stationary one but then to veer away either before or after contact was made between the two. In 7 cases both the moving and stationary flies moved apart. In 3 cases the stationary individual moved out of the path of the fly which was in motion. While the stationary flies tended to remain in position when approached by another fly, there was no case observed in which the stationary fly moved towards the approaching animal as if to drive it away. Such active defence is typical of verte-

brate territoriality. Another series of observations of 34 interactions between pairs of flies, both of which were walking over the surface of the paper, indicated a wider range of variability in behaviour. In 11 of the cases, as the two flies approached each other, one stopped while the second continued onward, although the path of the latter may or may not have been deflected. In 10 instances one of the two individuals turned from its path while the second did not. In 7 other cases both flies continued on their paths and bypassed each other. Finally, in 6 cases both flies altered their direction as they approached each other. Again, there was no evidence that a vertebrate-type of territorial behaviour existed.

The uniform spacing pattern maintained by the flies is regulated, at least in part, by avoidance reactions exhibited by the flies when they are within 1 to 5 mm. of each other. A fly is capable of controlling its immediately surrounding area to a limited extent by extending the legs and touching nearby flies (Plate III). This action results in the dispersion of one or of both animals so that they become more uniformly spaced over the surface. The maximum surface area which can be controlled in this manner is approximately 17 mm.^{2}, 9·3 mm.^{2} of which is occupied by the fly itself. The remaining space does not extend equally far on all sides of the fly for only areas in front of and alongside of the fly appear to be under control. As a result of these avoidance reactions, most flies remain at least two leg lengths distant from each other.

The uniform spacing pattern of *D. paramelanica* appears to have certain characteristics which distinguish it from the type of territoriality exhibited by most vertebrates. First, there is no defence of a specific area *per se* nor of a specific object (such as a harem in certain vertebrates) other than the fly itself. Secondly, the flies do not actively seek out and contact approaching flies. This appears to be especially true for those flies which are not moving.

There are a few apparent similarities between territoriality and the uniform spacing patterns displayed by *D. paramelanica*. Among many vertebrates, both sexes may define the territory; in unisexual populations, males as well as females of *D. paramelanica* space themselves relatively evenly. Two populations of males had R values of 1·34 and 1·40 at population levels of 148 and 176 individuals respectively. Furthermore, both uniform spacing and territoriality result in limiting the numbers of animals which can occupy an area.

The most plausible significance of the uniform spacing exhibited by *D. paramelanica* is related to the limitation of population levels and to the amount of unoccupied space surrounding the individuals of a population. *D. paramelanica* congregates from surrounding areas to fluxes on trees which are suitable for feeding and for ovipositing. It is well known from many other studies (e.g. Pearl, 1932) that biological activities such as egg production can be influenced by changes in population density in a bisexual population. At least one factor responsible for the decrease in egg production with increase in population density is the mutual interference of the animals at critical times, such as during copulation. Any system which would reduce the amount of serious interference, such as territoriality, uniform spacing, or social hierarchies, would be expected to alleviate the deleterious effects of crowding to some degree. It is conceivable that the system of uniform spacing present in a species such as *D. paramelanica*, a motile animal which moves from one slime flux to another in search of food, oviposition sites, etc., could act in such a manner that competition for food or for sites in which to lay eggs would be reduced.

Summary

1. The spacing patterns of females of *Drosophila paramelanica* hanging suspended from a moist filter paper were determined.

2. The females were relatively uniformly spaced. Within limits the mean distance between adjacent flies became more uniform as the population density increased from low levels. At higher densities the spacing pattern of the flies was relatively constant.

3. The number of flies capable of remaining on the filter paper was limited.

4. This limitation of the number of flies and the occurrence of the uniform spacing pattern of the flies are attributable to avoidance reactions made by flies when within 5 mm. of each other.

REFERENCES

Alexander, Richard D. (1959) Dominance-subordinance and territoriality in field crickets. *Bull. ecol. Soc. Amer.*, **40**, 120.

Clark, Philip J. & Evans, Francis C. (1954). Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecol.*, **35**, 445-453.

Free, J. B. (1958). Defence of bumble bee colonies. *Behaviour*, **12**, 233-242.

Jacobs, Merle E. (1955). Studies on territorialism and sexual selection in dragonflies. *Ecol.*, **36**, 566-586.

Naylor, Alfred (1959). An experimental analysis of dispersal in the flour beetle, *Tribolium confusum*. *Ecol.*, **40**, 453-465.

Pearl, Raymond (1932). The influence of density of population upon egg production in *Drosophila melanogaster*. *J. exp. Zool.*, **63**, 57-84.

Accepted for publication 12*th May*, 1960.

THE EFFECTS OF ARTIFICIAL SELECTION FOR MATING SPEED IN *Drosophila melanogaster*

By AUBREY MANNING

Department of Zoology, University of Edinburgh

Introduction

Artificial selection for behavioural features can be of considerable interest for two reasons. Firstly it is likely to yield information on the genetic basis of behaviour, and we still require much more of the basic data of behaviour genetics. Secondly one of the effects of selection may be to produce exaggerations of the normal system which reveal, by their interactions with other behaviour patterns, something of the underlying organization.

Among recent behavioural selection experiments have been those of Broadhurst (1958) using emotionality in rats, and Hirsch & Boudreau (1958) using phototactic responses in *Drosophila*. These, with the application of refined forms of genetic analysis, have yielded results of great interest from both behavioural and genetical standpoints.

Drosophila workers have often noticed the great variation in the time taken for virgin flies to mate when males and females are first mixed. Even when conditions are kept as standard as possible much variation is left, and the experiments to be described are an attempt to select out lines of *Drosophila* which mate more quickly or more slowly than normal. It is obvious that no single factor will emerge as the mediator of mating speed, but the effects of intense selection on the complex of factors involved may help to identify some of them and indicate those which are most easily changed.

Materials and Methods

The base stock of *D. melanogaster* I used was collected by Dr. Forbes Robertson some years ago and since maintained as a large population; it is known to be genetically diverse. The simple method used for selecting mating speed I also owe to Dr. Robertson. 50 pairs of virgin flies are mass mated in a half-pint milk bottle held horizontally in a clamp and with the only light coming from a 100W. bulb 18 inches from the closed end. The flies tend to gather at the light end and as courtship proceeds pairs can be sucked out with a "pooter" as soon as they copulate. This can be done without making them separate or disturbing the courtship of the other flies. I kept a record of the rate at which pairs mate for periods up to an hour or more as needed.

At the beginning of the experiment two identical groups (A & B) of 50 pairs from the base stock were mated and the first 10 and last 10 pairs to mate in each were bred in standard culture bottles. These constituted the parental generation of two fast (FA and FB) and two slow (SA and SB) mating lines. In subsequent generations 50 pairs from each stock were measured for mating speed and the 10 fastest pairs bred from each of the F-lines, the 10 slowest from each S-line. At intervals during the course of the experiments the mating speed of a sample from the unselected parent stock was measured for comparison.

The ten pairs of selected flies per bottle were removed after 24 hours to limit the number of eggs laid and the bottles were then given ample extra yeast suspension. Virgin flies were collected on the first, second and sometimes third day of hatching and the sexes aged separately in small groups in vials, being transferred to fresh food every other day. The day before testing they were etherized again and sorted into their groups of 50 ready for shaking into the testing bottles. Collecting flies over 2 or 3 days eliminated any chance of selection for rapid or slow development but meant that the groups tested consisted of flies of different ages. For this reason they were aged in vials until the youngest flies would be 4 days old when tested. There is evidence, (Manning, 1959a) that *melanogaster* females reach a peak of receptivity at 3 days of age, but that thereafter until perhaps 10 days old there is only a slight decline in their willingness to mate. Flies tested at 4, 5 and 6 days of age may thus be assumed to be quite homogeneous in their receptivity and age fluctuations will not hamper the course of selection for mating speed.

The flies were reared and the tests made at 25°C.

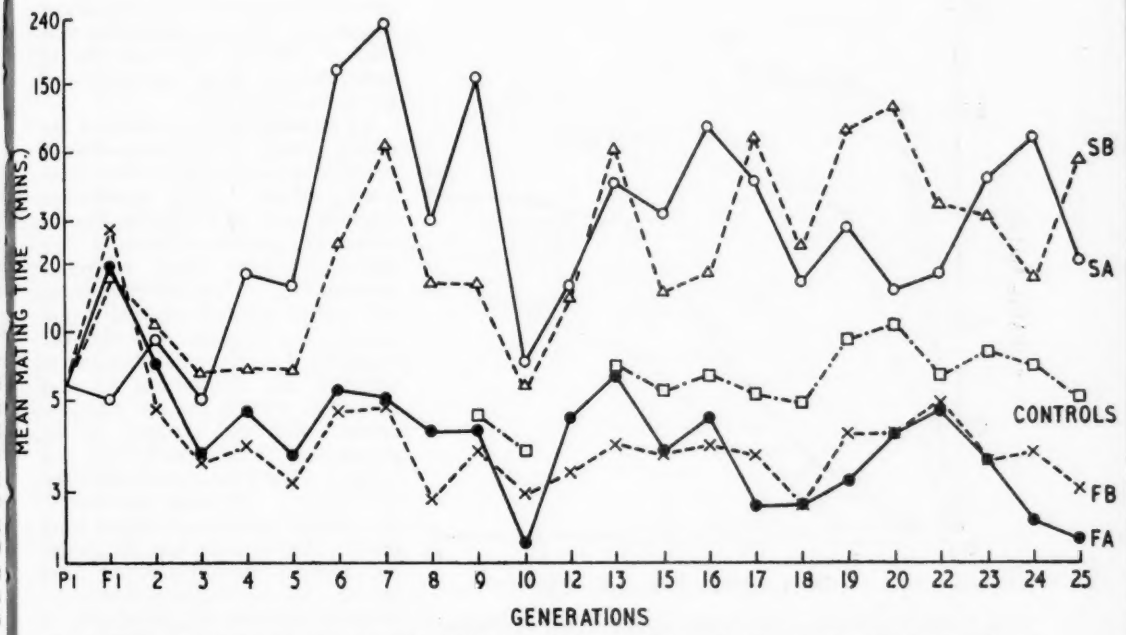


Fig. 1. The course of the response to selection for fast and slow mating speed. Mean mating time is plotted on a logarithmic scale. Selection was relaxed in generations 11, 14 and 21.

The Course of the Selection Response and Genetical Results

Fig. 1 shows graphs of the changes in mean mating times, (measured by a probit transformation, see p. 00) for successive generations of the selected lines and of controls when these were measured. The response to selection was almost immediate and from F2 onwards the S- and F-lines were quite separate. It continued for some 7 or 8 generations, but subsequently, with the possible exception of FA, little change in mating speed was produced. The relatively enormous fluctuations in mating speed between generations are conspicuous. These usually effect all the linesi n a parellel fashion; thus F3, 10 and 18 show fast speeds, whilst F6, 7 and 13 are all slow. It seems certain that these fluctuations are due to some common environmental factors, the nature of which are still obscure. This problem is of great interest, for it is often noted that *Drosophila* have their "on" and "off" days for courtship and hitherto temperature has been often the only well controlled factor.

Fig. 2 shows a complete record of the mating speeds during the selection test in F18. The differences were so great that about 70 per cent. (35 pairs) of the F- lines had mated within 2 minutes before even the first of the S-lines had done so. The unselected controls show an intermediate rate, but here, as in most generations, they are closer to the F- lines. In general it was true that selection had a greater effect towards slowness than rapidity. Rapid mating is probably a feature contributing to "biological fitness" and one would expect it to be held fairly close to the possible maximum by natural selection. Consequently this artificial selection for mating speed comes into line with other experiments on such features, where selection was less effective "up" than "down".

The genetical results of this experiment reveal nothing unexpected beyond a consistency and simplicity that might not be predicted. The measure used is, after all, the behavioural interaction between two individuals and is therefore exposed to a whole range of obscuring factors.

The results are consistent with the accumulation in the selected lines of many genes affecting mating speed. These blend their action smoothly

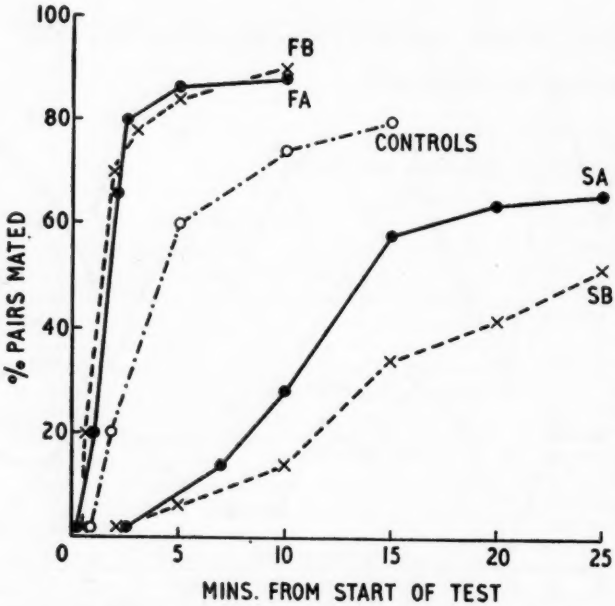


Fig. 2. Graphs of mating speed during the selection test on F18 flies.

in hybridizing F- and S- lines to produce F1 flies with roughly intermediate mating speeds, similar to that of controls. Fig. 3 shows the mating speed graphs of the F1 hybrids from F17 parents. The subsequent backcrosses show mating speeds intermediate between the F1 and the parent stock, with remarkably little overlap, Fig. 4. Hybrids between the two F- and the two S- lines, (which are also shown on Fig. 3) have mating speeds very similar to the parents and thus it appears that genes with similar actions have accumulated in each pair of lines.

For each line in every generation the percentage of pairs mated during the test was transformed into a probit and plotted against the logarithm of time since the test began. This transformation usually gave a good straight line plot, (which was fitted by eye) and thus an estimate of the mean mating speed and the standard deviation. These measures can at best only be approximate, for though each population shows a roughly normal distribution of mating speeds, conditions in the tests do not remain constant over the whole period. The last few pairs to mate do so under far less crowded conditions than the early pairs. However for the S- lines, where often only a few pairs had mated within a reasonable observation time, the probit/log. time plot is probably the best way of estimating the mean mating time of the 50 pair population.

To estimate the heritability of the mating speed, i.e. that proportion of the total variance which is due to the average effects of genes, the selection response must be plotted against the cumulative selective differential. This last is a figure which represents cumulatively the total selection pressure applied through successive generations to produce the observed response. It combines the intensity of selection—the proportion of flies chosen as parents for the next generation—with the variance of the population from which they are selected. Clearly the more variable the population is, the more the mean of the selected group will depart from the population mean and the greater the expected effect of selection. Thus the selection differential will be larger the more variable the population is for mating speed. (For a full acount of this and other methods of calculating heritabilities, see Falconer, 1960).

Since I omitted to measure controls over the first few generations of selection, when it was most effective, probably the best estimate of heritability is gained by measuring the rate at which the two pairs of selected lines diverge from one another. This is done in Fig. 5 where the difference between the mean mating speed of the two F- lines averaged and the two S- lines averaged is plotted against the mean selection differential accumulated over successive generations. The divergence increases rapidly for 7 generations and then begins to fluctuate but with little sign of further progress—essentially the same picture as revealed by Fig. 1. The slope of the regression line fitted to the points during the initial divergence gives a direct measure of the "realized" or "cumulative" heritability. There is perhaps little reality in the heritability of a character which involves the interaction between two individuals. However the consistency of selection's effect and the fact that the accumulated genes appear to affect males and females in a behaviourally complementary fashion, make it worthwhile to fit a regression line and simply state that the heritability is approximately 0·30.

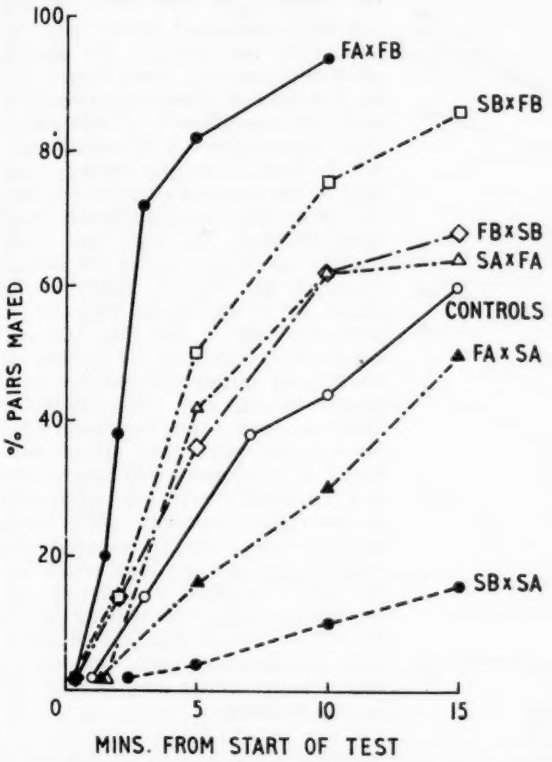


Fig. 3. The mating speeds of F1 hybrids from F17 parents. The male parent's line given first in each case.

Since the response is greater in the direction of slow than of fast mating, the larger part of this figure will be due to the S- lines. In a repeat of this experiment it will be more interesting to measure the heritabilities of mating speed in the two sexes separately by measuring a sample of each against controls in every generation.

There is no doubt that considerable variability for genes affecting mating speed still remains in the selected lines. Reversed selection, i.e. breeding from the fastest mating pairs of the S- lines and the slowest of the F- lines, was begun in F15. Within 7 generations the mean mating speeds of all four lines were back to levels very close to that of controls. This experiment should, perhaps, have been continued until the levels "crossed", but it was already clear that the reverse-selected lines were not the same as before in behaviour. Reversed selection can rarely restore the genetical *status quo* for of necessity it is acting upon a changed genotype. Analogously the behaviour too was altered and, for example, the reverse-selected fast mating lines came to include increasing numbers of extremely inactive flies which scarcely moved throughout the test and mated slowly for this reason (see p. 00).

If variability remains in the selected lines one would predict that on relaxing selection, or rather returning to natural selection alone, the lines will revert to their previous state since one is bound to have disturbed their naturally selected optimum genotype. Samples of the four lines have now been bred without artificial selection for 15 generations, beginning as with counter selection from F15 parents. These relaxed lines have fluctuated widely in mating speed, as have the lines with continued selection, but are still little closer to controls than at the outset. The most likely reason for this stability is not lack of genetic variability but lack of natural selection pressure. The conditions in the stock bottles with good food conditions are such that selection pressures against the fast and slow mating genotypes are slight.

Phenotypic variability, on the other hand, has been greatly changed as a result of the selection. The mating time of 50 pairs of the F- lines is compressed into a period of 3 to 4 minutes, whilst the same number of control flies take 10 minutes or more. The S- lines are far more variable, for selection has not produced flies which have a long delay until the first mating, but which subsequently all mate within a short time. Nearly always one or two pairs are mated within the first few minutes but the rest may be spread out over 2 hours or even longer.

General Effects of Behaviour

Hybridizing the S- and F- lines has shown that they produce an F1 with an intermediate mating speed. It is of interest to see whether a similar intermediate speed is obtained when males from an F- line are courting S- line females and *vice versa*. Accordingly the mating speeds of such crosses were measured at various stages from F7 onwards. Fig. 6 shows a typical result from F7 and the speeds are indeed intermediate, whilst intercrossing the two F- and the two S- lines in this way produces fast and slow speeds respectively.

These results confirm those from hybridiz-

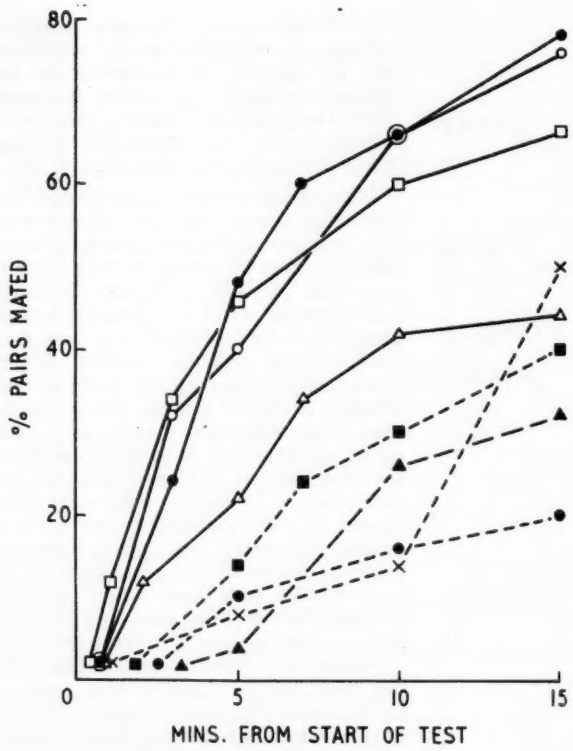


Fig. 4. The mating speeds of F2 backcrosses from the hybrids between F— and S-lines shown in Fig. 3. Backcrosses to the fast parent are solid lines, those to the slow parent are broken lines.

ation in showing that the changes produced by selection have been similar in both pairs of lines, and further that both sexes have been affected. An independent measure of this was obtained by testing mating speeds against an unselected stock which was equally "foreign" to the normal controls and the selected lines. Fig. 7 shows the results taking samples for F18, all flies being 3 days old when tested. The selected lines and controls occupy the same relative positions as when mated within their own stock, though the S- line females mate rather faster with the foreign males than might be expected.

The Nature of the Behavioural Changes

A large number of factors might be responsible for changing the mating speed of *Drosophila*. Apart from showing that some of them have an inherited basis this experiment is of little behavioural interest unless it manages to narrow the field. It became obvious quite early in the course of selection that features other than sexual behaviour were being affected. The light was made strongly directional during the tests to encourage the flies to gather at the closed end of the bottle. After 3 or 4 generations the F- line flies were still congregating closely but the S-lines were much more spread out and not so attracted by the light. This inevitably leads to slowed mating for contacts between males and females are reduced. Hirsch & Boudreau (1958) have shown how readily the phototaxis of *melanogaster* responds to selection and it seems probable that, initially, selection for mating speed can act most readily via the natural variation in phototaxis and its resultant effects on spacing out in the test bottles. As selection proceeded these changes were soon obscured as other features with a greater effect began to respond.

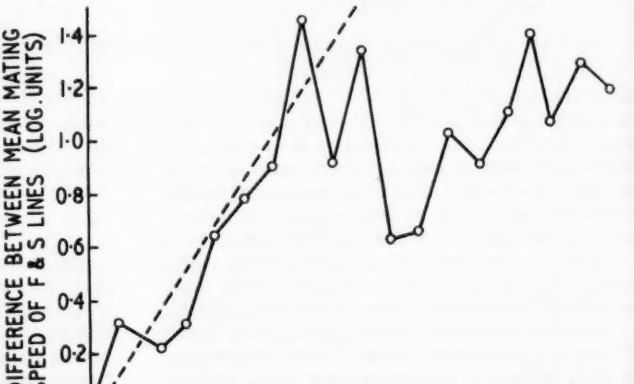


Fig. 5. The divergence between F- and S-lines plotted against the mean cumulative selection differential. The regression line fitted to the graph up to and including F7 is shown. Its slope gives a measure of the heritability, approximately 0·30.

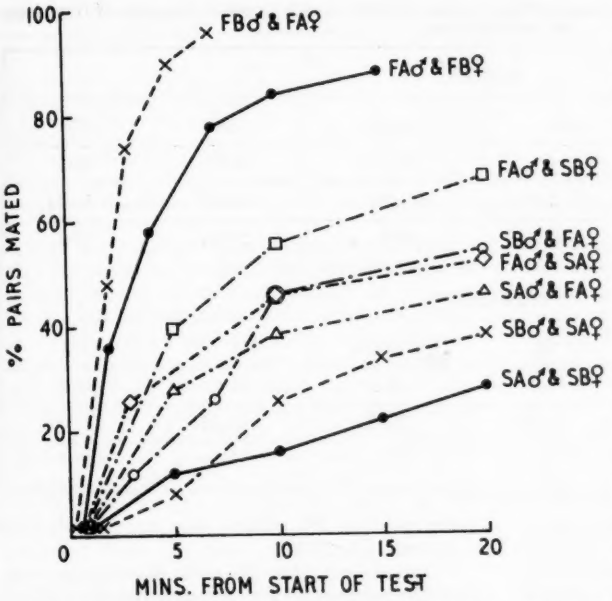


Fig. 6. The mating speeds which result from mixing males and females between the lines. The flies are all from F7.

The most noticeable of these related to the general activity of the flies. By as early as F6 it became clear that flies of the S- and F- lines had very different patterns of activity. Whilst ageing in the vials S- line flies would react strongly to any disturbance but the F- lines were markedly sluggish. These differences reflected themselves in the behaviour when testing and had great effects on the mating speed. When first shaken into the bottle the S- line flies showed 1 to 3 minutes, or even more, of violent activity, running and flying around in a random fashion unrelated to the direction of the light. This meant that males did not begin courting persistently for 3 or more minutes. On the other hand the F- lines showed little disturbance when put into the bottles and courtship began immediately. It is difficult to define "general activity" at all precisely in *Drosophila* but as measured here it means, locomotor activity released by any environmental stimuli other than sexual ones. Some of it has the appearance of being "spontaneous" but this is difficult to prove. Activity is highest following introduction to a new environment and might have something in common with "exploratory behaviour" in vertebrates. Certainly *Drosophila* species show characteristic activity levels. *Melanogaster*, for example, is far more active than its close relative *simulans*, (Manning, 1959b) and stocks of the same species often appear to differ in this respect.

To get some kind of objective criterion of activity differences between the selected lines, flies were tested in an open arena. This was made of perspex, 10×10×1 cm. deep with its roof, floor and walls marked off in 1 cm. squares. It was lit by fairly powerful diffused light from above and the flies were introduced singly into a small box with access by a moveable screen to the middle of one side of the arena. After a pause of some 15 seconds in the starting box, the screen was raised and the number of cm. squares the fly entered, (whether on roof, floor or sides) within 1 minute from crossing the screen was counted. At 3 days of age 5 flies of each sex from each of the selected lines and the control stock were tested this way for 4 successive generations, (F16-19) and Table I summarises the results.

There was a great deal of variation within lines, at least partly due to inevitable differences in disturbance when introducing flies to the starting box. There were also inter-generation differences significant between 5 and 1 per cent. levels in the case of males, but the inter-line differences were constant. Comparing the variance between lines the results are similar for both sexes and show:—1. The two S- lines show similar activity levels, as do the two F- lines, but that of the S- lines is higher, ($P<0{\cdot}001$).

2. Control flies show no significant difference from the S- lines in activity.

The averages of squares entered gives a very clear picture of the differences between the F- and S- lines. S- line flies were moving in the arena for the majority of the minute test, with short pauses when they cleaned themselves. F- line flies often only moved a few squares past the screen and then remained still, though often cleaning, for the rest of the test.

It was mentioned that the most obvious effect of activity upon mating speed was to increase the length of disturbance following introduction to the test bottle and thereby delay the onset of courtship. A more accurate measure

Table I. The Number of Squares in the Arena Entered within 1 minute. 20 Flies in each Group, 5 from each of Generations 16 to 19 inclusive.

MALES					
	SA	SB	Controls	FA	FB
Mean squares entered	59·8	54·6	49·1	24·8	20·2
Range	23—99	17—125	4—103	1—51	2—61
s	19·5	27·8	26·9	15·4	18·8
FEMALES					
	SA	SB	Controls	FA	FB
Mean squares entered	50·3	46·5	43·1	21·6	13·2
Range	1—101	8—89	13—75	1—36	1—36
s	27·3	24·9	18·3	13·1	11·3

of this effect was obtained by timing the delay before courtship in single pair matings made in small observation cell, 1 inch in diameter. Here a stock female (equally "foreign" to selected lines and controls) was placed in a cell and allowed to settle before introducing the male to be tested. The time from his introduction to the beginning of courtship (the so-called "lag time") was measured to the nearest 5 seconds for 20 matings of 3 day old males of each line and controls from F9. The results are summarised in Table II.

An analysis of variance shows significant differences between lines and comparing the means of samples with the within sample variance shows the following results:

1. SA males have longer lags than SB, ($P<0·0001$). This is due to a few extremely long lags in the former sample.

2. SB males have lags significantly longer than those of control males, ($P<0·001$).

3. Control and FA males do not differ in this respect, nor FA and FB, but on these figures control and FB males are just significantly different, ($P<0·05$).

Thus the actual order of the lines based on the activity measure, (SA, SB, control, FA, FB) is exactly paralleled by average lag time. However in activity control flies were similar to the S-lines, but in lag time they resemble the F- lines. The chief difference in the two situations is that the arena offers no sexual stimuli, whilst lag time is probably a measure of the time taken for sexual stimuli from the female to overcome the effects of "activity stimuli" from the new environment of the cell. Accordingly it was necessary to see if there are any differences in the sexual responses of the different lines.

This was done by recording the courtship of the males following the lag-period measurements just described. The "licking" movement, in which the male extends his proboscis towards the female's ovipositor gives a simple criterion of the courtship. Bastock & Manning (1955) showed that the frequency of licking is positively correlated with the length of bouts of wing

Table II. The Lag-periods Before Courtship in 20 3-day old Males from Each Group in F9.

	SA	SB	Controls	FA	FB
Mean lag periods (seconds)	73·8	41·5	19·5	13·5	9·3
Range	20—240	5—125	5—95	5—50	5—40
s	2·9	37·5	21·8	14·6	8·1

Table III. The Frequency of Licking Expressed as a Fraction of 100 seconds of courtship for 20 males of each Group from F9.

	SA	SB	Controls	FA	FB
Mean frequency of licking	9·1	10·5	14·3	13·6	13·6
Range	1—17	6—15	5—22	6—19	6—28
s	3·67	2·69	4·74	3·25	5·09

display and thus provides a measure of "courtship intensity" as a whole. The females used in these tests were, as mentioned above, of another stock from the unselected control flies and were 1-day old when tested. This meant that though attractive to males, they were not very receptive and courtships were of adequate length for recording. No courtship of less than 100 seconds was counted and a sample of 200 seconds was taken wherever possible. The results are summarized in Table III. The amount of licking is expressed as the average frequency in 100 seconds of courtship, (breaks in courtship being excluded from the time count) and since the movement itself lasts for about a second the measure approximates to a percentage of time spent licking.

The test was made initially on males from F9 and shows clearly that the S- line males have a poorer, lower intensity courtship than controls or F- lines. The difference in licking frequency between the best S- line (SB) and either F- line or controls is significant at the 0·1 per cent. level. A similar test with F17 males gave the same result with even less overlap in the range of licking frequencies between the lines. In F27 a further check of the two extreme lines, (at this stage) SA and FA together with controls revealed mean licking frequencies of 6·37, 13·56 and 11·50 respectively with 16 males per group. Here FA has a significantly better performance than the control line, $P<0{\cdot}001$. A small difference in the licking frequency represents a considerable difference in the amount of wing display in the courtship and the deficiencies of the S- line males in this respect are probably quite sufficient to account for their poor success.

The short lag-periods and high frequency of licking in the courtship of F- line males both indicate that the sexual response threshold is lowered. There were other signs that this was so. F- line males courted with extreme persistence and frequently spent long periods directing their courtship to other objects in the observation cells. They courted the peg which seals the entrance hole, or courted their own reflection in the cover slip over the top of the cell. These rarely proved adequate stimuli for the control or S- line males.

The changes in female sexual behaviour are more difficult to distinguish from changes in activity levels. The behaviour of a receptive female is to stand still or walk slowly when a male courts, and the F- line females all did this. An unreceptive female may, whilst standing still, flick her wings, kick backwards or extrude her ovipositor, but she may also decamp, jumping or flying right away. S- line females most commonly took the latter course and there was a great amount of flying and jumping in the test bottles. With both types of female, it is difficult to say how far their behaviour towards males simply reflects their differential reactiveness to disturbing stimuli or whether it is a purely sexual response. However, comparing repelling movements made whilst relatively still, there was certainly more ovipositor extrusion from S- line females, a movement of sexual rejection, presumably representing a raised sexual response threshold.

Discussion

We may summarize the behavioural differences between the lines as follows:

1. The S- lines show a high level of activity. The males have long lag periods before courtship and a reduced frequency of licking in their courtship. The males have a correspondingly reduced success with foreign stock females (Fig. 7a) and the females show lowered receptivity and require more courtship before accepting stock males (Fig. 7b).

2. The F- lines have a greatly reduced level of activity. The males have short lags before courtship and a licking frequency equal to, or better than that of controls. They have increased success with stock females and conversely the females mate rapidly with stock males.

3. Unselected control flies show a high level of activity, yet their lags are quite short and the

Fig. 7. The mating speeds of, (*a*) selected line and control males with stock females, (*b*) stock males with selected line and control females. The flies are all from F18.

males show high intensity courtship. They show intermediate success with stock females, and control females have an intermediate speed of mating with stock males.

Briefly then, whilst the S- lines show high activity and low sex, the F- lines show low activity and high sex, but the controls show both high activity and high sex. It appears that selection has been most successful in directions based upon raising the thresholds of performance. The most conspicuous effects are the raising of the activity threshold in the F- lines and that of courtship in the S- lines. This indicates in turn that under normal domesticated conditions, in a population cage or stock bottle, "natural" selection keeps the levels of general activity and sexual behaviour near to the possible maximum. However smaller changes towards lowering reaction thresholds have been produced. The S- lines show signs of becoming hyperactive and the most recent test of male sexual behaviour showed FA to be "better" than the controls.

It certainly appears that the differences in activity between the selected lines are just as important in altering the speed of mating as the direct changes to sexual behaviour. It is not so much the level of activity that matters as the speed with which the fly can make the change over from activity responses to sexual ones. Shaking into the test bottle provides powerful activity stimuli and at the same time brings the sexes together and provides sexual stimuli. To this mixed stimulus situation the S- lines respond with violent activity and though there are frequent encounters between males and females, no sexual behaviour is released for some minutes. The F- lines with their low activity scarcely respond to the disturbance, males begin to court when they first meet a female and within a few seconds the first pairs have mated. Control flies, though they show a high activity level in the arena tests, show only a brief burst of activity when shaken into the test bottle. The switch to sexual behaviour is rapid, almost as quick as in the F- lines, and mating speed is correspondingly fast. Activity and sexual behaviour are mutually incompatible and a speedy change over to the latter must depend on the threshold for sexual behaviour being low, as it is in both controls and F- lines. The raised sexual threshold in the S- lines results in a greatly lengthened initial period of activity. Conversely the raised activity threshold of the F- lines reduces this period almost to nothing. The control flies have established under natural selection optimum levels of activity and sexual behaviour which leaves them adequately responsive to both types of stimulus. It will be interesting to examine the response levels of flies newly caught in the wild.

There is clearly a limit beyond which further reduction in activity does not result in faster mating. This point was passed by the reverse-selected fast lines, as mentioned on p. 00. During tests FA and FB usually had some 30 or 40 pairs mated within 3 minutes, but the remaining few pairs took much longer. These flies were often completely motionless for minutes on end and consequently no sexual encounters took place to initiate courtship. Tapping the bottle sometimes produced enough disturbance to bring males and females together again. It is these exceptionally inactive flies, since they are last to mate, which are bred from during reversed selection and they tended to increase in numbers. Hence reversed selection, though effective in reducing mating speed, did not retrace the path to a state like that of the controls.

For an understanding of the organization of *Drosophila* behaviour it is important that the artificial selection pressure applied here has resulted in a separation of those systems concerned with "general activity" and sexual behaviour. It is often assumed that a "vigorous" insect displays this quality in all aspects of its behaviour. This is just the argument I used to account for the observed differences between the behaviour of *D. melanogaster* and *D. simulans* (1959b), and certainly activity and sexual responses appear to decline together when flies are inbred. Normally natural selection may cause the two to be positively correlated as in my control line. However artificial selection has produced very active flies with a less vigorous form of courtship and also very sluggish flies that nevertheless show great vigour when courting. Clearly a simple concept of "vigour" is not sufficient.

The physiological bases of these behavioural differences have not yet been investigated and this may prove very difficult. One can easily imagine that the decrease in both activity and sexual behaviour which occurs on inbreeding is due to a depression of the insect's total metabolism, but such cannot be the case here. There are various facts which tell against any general metabolic changes. The development time of all the selected lines has remained the same as controls throughout the experiment. Dr. Forbes

Robertson kindly measured the egg production of all four lines, which is likely to be very sensitive to changed metabolic conditions, and finds no difference from controls. Again, Dr. Margaret Bastock finds that F- and S- lines perform equally well with controls in forced flight tests—a good measure of muscular efficiency and endurance. The most likely conclusion is that the genes accumulated in the selected lines are affecting neural thresholds in mechanisms concerned with the control of sexual behaviour and of responses to other environmental stimuli.

Summary

1. This paper describes an experiment in which lines of *Drosophila melanogaster* were selected for fast and slow mating speed over some 25 generations.

2. After 7 generations selection had produced a divergence in mating speed such that the mean speed of a 50 pair population was about 80 minutes in the slow mating (S) lines but only 3 minutes in the fast (F) lines. Subsequently selection made little progress though there have been wide fluctuations in speed, probably environmentally determined.

3. Hybridizing S- and F- lines produces an F1 with intermediate mating speed. Other tests show that the behaviour of both sexes has been altered in a complementary fashion.

4. As measured in an open arena, the general activity of S- line flies is much greater than that of the F- lines and unselected controls resemble the S- lines in this respect. Measurements of the sexual behaviour of males show that the F- lines and controls have a higher intensity courtship than the S- line males.

5. The most conspicuous effects of selection are to raise the reaction thresholds of sexual behaviour in the S- lines and of general activity in the F- lines. To situations involving a mixture of both sexual and activity stimuli, the S- lines respond with prolonged activity but the F- lines show scarcely any and begin courtship immediately. Controls show a brief burst of activity but rapidly change over to courtship.

6. Natural selection will normally lead to the levels of activity and sexual behaviour being positively correlated and at an optimum which does not result in over-responsiveness in either direction. Artificial selection has led to a separation of the two systems and no concept of a "vigour" which inevitably affects all behavioural levels is adequate.

7. There are no signs of general metabolic changes to the selected lines and it is probably that the accumulated genes affect thresholds in the nervous system.

Acknowledgments

I am most grateful to Dr. Forbes Robertson, Dr. D. S. Falconer and Dr. Margaret Bastock for help and advice at all stages of this work.

REFERENCES

Bastock, M. & Manning, A. (1955). The courtship of *Drosophila melanogaster*. *Behaviour*, **8**, 85-111.

Broadhurst, P. L. (1958). Studies in psychogenetics: The quantitative inheritance of behaviour in rats investigated by selective and cross-breeding. *Bull. Brit. Psychol. Soc.*, **34**, 2A (abstract).

Falconer, D. S. (1960). *Introduction to Quantitative Genetics*. Edinburgh & London: Oliver & Boyd.

Hirsch, J. & Boudreau, J. C. (1958). Studies in experimental behavior genetics: I. The heritability of phototaxis in a population of *Drosophila melanogaster*. *J. comp. physiol. Psychol.*, **51**, 647-651.

Manning, A. (1959a). The sexual isolation between *Drosophila melanogaster* and *Drosophila simulans*. *Anim. Behaviour*, **7**, 60-65.

Manning, A. (1959b). The sexual behaviour of two sibling *Drosophila* species. *Behaviour*, **15**, 123-145.

Accepted for publication 31*st August*, 1960.

BODY SIZE AND COURTSHIP BEHAVIOUR IN *Drosophila melanogaster**

By ARTHUR W. EWING

Department of Zoology, University of Edinburgh

Introduction

Most of the changes occurring in animal populations due to natural selection are the result of selection pressure acting on quantitative characters which are multifactorially controlled. Some of these changes although not primarily behavioural, could have an effect on the animal's behaviour and it is therefore of interest to examine populations of animals which have been selected for such characters to try to discover what type of change could occur. An ideal opportunity arose to study this problem in lines of *Drosophila melanogaster* which had been selected for large and small body size. Dr. F. W. Robertson, in the course of selecting these lines, had noticed that they differed in the time that they took to mate. A preliminary examination of the lines revealed differences in their courtship and this paper describes the investigation of these differences and some analysis of their causation.

Materials and Methods

Initially four selected lines were examined, two having been selected for large body size (PAL, PBL) and two for small (PAS, PBS), control being the base stock (PAC) from which the selected lines originated. The criterion of thorax length rather than that of overall body size was used as a basis of selection as the former provides a more convenient measure and is correlated with body size. The lines were obtained from Dr. F. W. Robertson and selection was continued using his techniques. The thorax lengths of 100 pairs of flies from each selected line were measured and the lines were continued with the ten largest and ten smallest pairs respectively. The selected ten pairs were intoduced into half-pint culture bottles containing standard Drosphila media and were allowed to mate at random and lay eggs for two days.

Fig. 1 shows a typical experiment of two-way selection from a base stock. Although the graph does not show the final result a plateau is reached after approximately 25 generations when the increase in thorax length is about 10 per cent. and the decrease 13 per cent. A more complete description of selection methods and a discussion of the genetical results of similar selection experiments is given by Robertson (1952, 1955). The following are the mean divergences of thorax length from control over the five generations (generations 9-13) that the experiment covered: PAL+8·9 per cent., PBL+6·8 per cent., PAS —8·4 per cent., PBS —6·3 per cent.

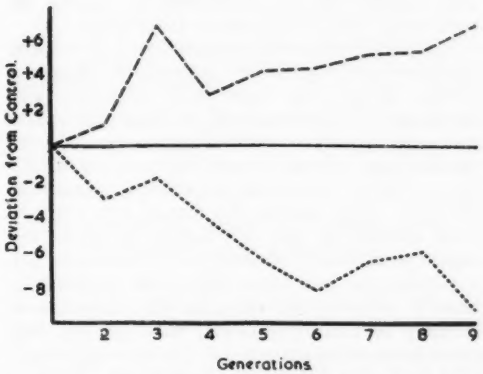


Fig. 1. The result of two-way selection of body size. Percentage deviation of thorax length is plotted against generation.

As many environmental conditions as possible were controlled both during the pre-adult stages and during the actual experiments. Stocks were kept in a constant temperature room at 28±1°C. and the illumination was provided by two 100 watt lamps which were switched on automatically at 9 a.m. and off at 11.30 p.m. Virgin flies were collected three times daily and matured in vials with a supply of fresh food, ten flies per vial.

All behavioural observations were also carried out in the constant temperature room between the hours of 9 and 12.30 in the morning, three-day-old flies being used throughout. The humidity in the observation cells was kept as high as possible by means of a plug of moistened cotton wool inserted into an aperture in the cell wall. All the experiments were spread over a minimum

*This investigation was supported by a research grant from the Department of Scientific and Industrial Research.

of two generations to eliminate any one-sided effects due to unequal culture conditions.

The method of recording male courtship was essentially similar to that of Bastock & Manning (1955). Pairs of flies were confined to perspex cells one inch in diameter and one quarter of an inch deep and were watched through a low power binocular microscope. Their courtship activity was recorded by means of a simple code, on a typewriter, every 1·5 seconds, the time intervals being indicated by a metronome. Approximately 2·5 minutes of actual courtship (i.e. 100 units of courtship) were recorded for each pair. This method seems to ensure a fairly accurate picture of the pattern of male courtship as larger samples do not materially affect the measures obtained. Males were always tested with control females in order to provide as constant a stimulus situation as possible.

A full description of the courtship of *Drosophila melanogaster* is given by Bastokc & Manning (1955). Briefly, the three basic courtship elements are: (i) orientation, in which the male takes up a position with his head towards the female and follows closely behind her if she moves off; (ii) vibration, in which the male extends the wing nearest the female and vibrates it up and down; and (iii) licking, in which the male extends his proboscis and attempts to lick the female's genitalia. The last element is usually followed by an attempted copulation. Bastock & Manning (1955) have shown that persistence of courtship and the bout lengths of vibration plus licking are correlated. Further, they have shown that percentage licking and bout length of vibration are also correlated. From this and other evidence we can regard the three elements, orientation, vibration and licking, as indicative of increasing thresholds of sexual excitation. Sturtevant (1915) and Bastock (1956) have demonstrated that vibration has a very important role in stimulating the female to a state of readiness to mate. Therefore flies that show large amounts of vibration in their courtship can be said to exhibit "high intensity courtship" and might be expected to be most successful in obtaining mates.

Courtship of the Selected Lines

Results

Twenty males from each selected line and control were examined using the method of courtship analysis described above. Fig. 2 shows the mean percentages of the three courtship elements for each of the lines when males

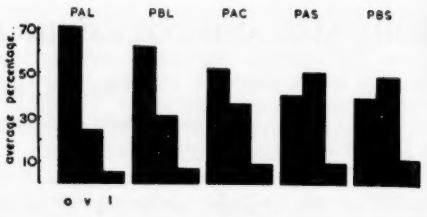


Fig. 2. The histograms demonstrate diagrammatically the average percentages of the three main courtship elements in the four selected lines and control: o = orientation, v = vibration, l = licking.

are courting PAC females. A small sample of five males from each line was also examined courting their own females in order to eliminate the possibility that the differences obtained were due to a differential response of the selected males to the control females. As can be seen from Fig. 3 approximately the same order of difference is found under these conditions.

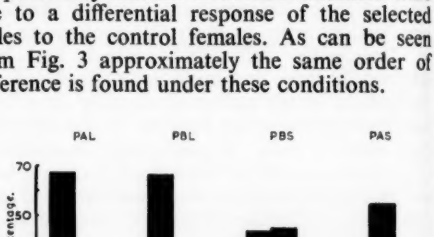


Fig. 3. As in Fig. 2 but the males are courting their 'own' females not control ones.

A between—and within—samples analysis of variance of percentage orientation and vibration showed that there is significantly more orientation and less vibration in the courtship of males from both the large lines, PAL and PBL, than in those from the small lines, PAS and PBS ($P<0{\cdot}1$ per cent.). Also the mean percentage of all three courtship elements in the control, PAC, males falls between that of the two large and small lines. Between both the small lines and control the differences in percentage orientation and vibration are significant at the 5 per cent. level, between PAL and control at the 0·1 per cent. level and between PBL and control at the 5 per cent. level. There are no significant differences between PAL and PBL or between PAS and PBS.

Two further lines selected for extremes of body size, PPL and PPS, were also examined and the same type of divergence in courtship

was again found, the large males exhibiting less vibration and more orientation than the small; control again being intermediate between them.

Thus in three replicate pairs of lines selected for extremes of body size a parallel divergence in courtship behaviour has occurred. The remainder of this paper describes an attempt to analyse the reasons for this divergence. The following possibilities were examined:

1. There could be a straightforward connection between phenotypic body size and courtship behaviour. Change in body size, regardless of its cause, would result in the type of courtship divergence found in the selected lines.

2. The genes controlling body size, or linked genes, might also affect courtship behaviour.

3. Selection may have had an effect on the lines' general level of activity and this could result in changed courtship behaviour.

4. Change in body size could affect courtship efficiency and thus create a selection pressure for changed male courtship.

Phenotypic Body Size and Courtship Behaviour

Although it is not possible, by altering the environment, to increase body size beyond the limits found in the control stocks which are kept under optimal conditions, the reverse is possible. Size can be reduced by rearing the larvae under crowded conditions such that there is competition for food. I therefore tested whether such "environmentally" small flies' courtship was similar to that of the small selected males (PAS, PBS, PPS).

Method

Two sets of vials were set up. In each of the first, one pair of flies was introduced and allowed to mate and lay eggs for one day. In each of the second set of vials were 15 pairs of flies which were allowed to lay for three days. Male progeny obtained from the latter crowded conditions were, on the average, 9·6 per cent. smaller in thorax length than the uncrowded flies and there was no overlap between the two classes with respect to this measure. The flies from the crowded conditions appeared perfectly normal and in no way sickly and it seems likely that under natural conditions competition for food between the larvae would be the usual situation rather than an overabundance of food. The experiment was done twice and the courtship of ten males from each class examined each time.

Results

The average percentages of the three courtship elements for the "environmentally" small and the normal males are shown in Fig. 4. The courtship of the "environmentally" small males resembles not that of the small selected

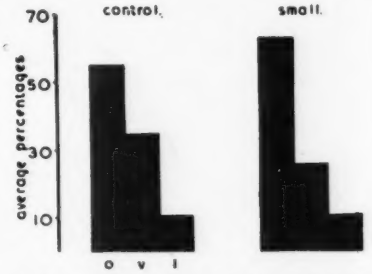


Fig. 4. A diagrammatic representation of the percentage of courtship elements in 'environmentally' small males as compared with control.

males but that of the large selected ones, exhibiting more orientation and less vibration than the controls. The difference is significant at the 1·0 per cent. level.

The Pleiotropic Effect on Courtship of the Genes Controlling Body Size

The following experiment was carried out to examine the second possibility listed, namely that the genes controlling body size (or closely linked genes) are having a pleiotropic effect on courtship behaviour. At the same time this experiment is a further test as to whether body size and courtship are phenotypically connected.

Method

The courtship of 34 male F2 progeny from crosses between the large (PAL and PBL) and small (PAS and PBS) lines was recorded and the percentage orientation calculated for each male. The thorax length of each male was then measured and plotted against percentage orientation.

Results

Independent reassortment of genes in the F2 generation results in variation of thorax length that almost includes the range in size between the large and small selected lines. The courtship behaviour also varies between the extremes found in the selected lines. If courtship is being influenced by the same genes that are controlling body size then these two aspects should be related in the F2 progeny, i.e. thorax length should

be negatively correlated with percentage vibration and positively with percentage orientation. Fig. 5 shows the result of plotting thorax length against percentage orientation and a regression

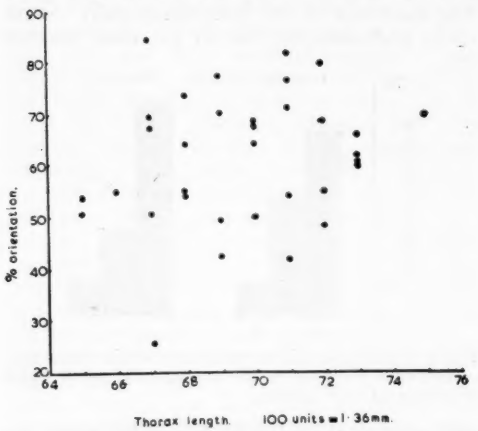


Fig. 5. Percentage orientation plotted against thorax length for the F_2 progeny of crosses between the large and small selected lines.

analysis gives an F value of 1·08 suggesting no degree of correlation. It therefore seems unlikely that the divergence in courtship behaviour is caused by the pleitropic effect of the genes controlling body size. The experiment also reinforces, and extends to the large flies, the conclusion from the previous experiment that the changes in courtship behaviour in the selected lines are not merely a reflection of phenotypic body size.

Courtship and Activity

In the unselected stocks natural selection maintains body size over a small optimum range and selection away from this optimum would be expected to affect other characters such as physiological efficiency or metabolic rate. If these characters were displaced from their optimal values there might be repercussions on courtship behaviour. A general measure such as that of activity would almost certainly reflect physiological or metabolic changes and this was therefore measured in the four selected lines and control.

Method of Measuring General Activity

The apparatus shown in Fig. 6 was designed to measure activity. Five male flies were introduced into the cell O and, after a period of about 30 seconds to allow the flies to recover from being manipulated, the gate A was removed allowing them to run into the five lanes separated by the partitions, B. After ten seconds the number of flies remaining in the cell and those in the regions 0-2, 2-4 and 4-6 inches from the gate were counted.

A light giving 300 ft. cdls./sq. ft. directly above the apparatus was the only source of illumination. A criticism of this method is that it does not eliminate interaction between the flies but other lines have been tested in this apparatus and in another designed to remove this setback and exactly parallel results were obtained from the two methods.

Results

The activity of the four selected lines, PAL, PBL, PAS and PBS and control, PAC, was measured using 100 males from each. Fig. 7 shows the figures obtained. An analysis of variance showed that all the selected lines were

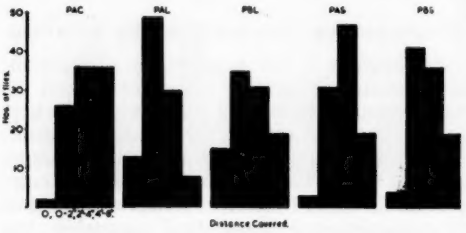


Fig. 7. The results of the activity measurements for the four selected lines and control. The horizontal axis represents the distance covered, and the vertical the number of flies.

less active than the control. The levels of significance were: for PAL, $p<\cdot01$ per cent., PBL, $p<1\cdot0$ per cent., PAS, $p<0\cdot1$ per cent., and PBS, $p<5\cdot0$ per cent. These differences in activity do not, however, explain the divergence in courtship behaviour. It is possible that with the large males their sluggishness and "low intensity" courtship may be connected but this is not applicable to the small males, which, in spite of being less active than the controls, nevertheless exhibit a "higher intensity" courtship.

Selection Effect J

The previous three experiments indicate that the divergence in courtship behaviour in the

PLATE IV

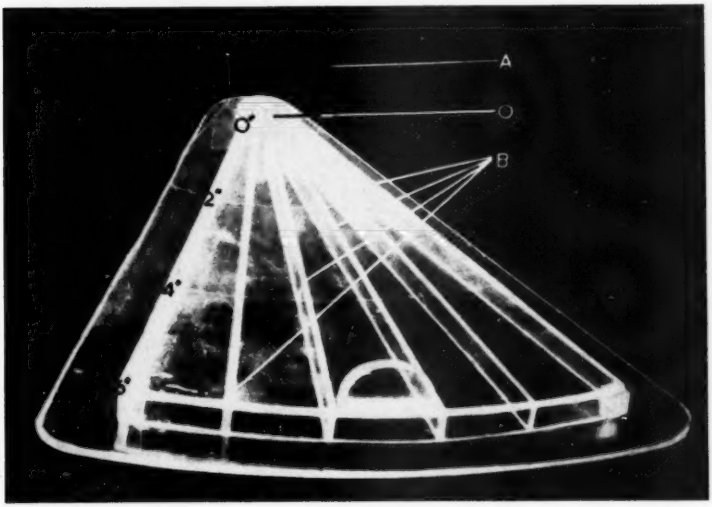


Fig. 6. Apparatus used in measuring general activity. A description of its use is given in the text.

selected lines cannot be attributed to any straightforward correlate of body size. Therefore the fourth possibility, namely that there had been selection for changed courtship, was examined. Little is known of the quantitative aspects of the stimulation in the courtship of *D. melanogaster*. Removal of the wings from males results in a very substantial increase in courtship time (Sturtevant, 1915). It is possible to conceive that increase or decrease in body size (and correspondingly of wing area) could affect the quantitative aspects of sexual stimulation. One way in which this would be reflected is the relative mating success of the lines. To test this the following "female choice" experiment was done.

Method

The males of one large (PAL), one small (PPS) line and control (PAC) were compared for mating success. These lines were chosen because the differences in courtship were greatest between them. The comparisons were done by pairs, PAL males being compared with PPS males, PAL with PAC and PPS with PAC. Five males at a time from each of the (pair of) lines being tested were placed in a 2×1 inch vial along with five females from one of the lines and the copulations scored. This was repeated until approximately 45 copulations were obtained in each class.

Results

Table I shows the results of these experiments. The main fact that emerges is that small males are less successful than either the control or the large males. Also interesting is the tendency for small males to be more successful with their own than with "foreign" females. This suggests that the relative sizes of male and female are important. As a check, comparisons were also made between PAL and PAS and between PBL and PBS and again the large males were more successful in obtaining mates than the small.

The design of the choice experiment is such that the difference in the amount of vibration exhibited by males tends to be reduced in importance. In the confined space of the vials males frequently change from courting one female to another and males with little vibration benefit from those that show more. This has been shown by Sturtevant (1915) who demonstrated that the sexual success of wingless males is increased when they are mixed with normal ones. The present experiment suggests that the courtship of the small males is deficient in respects other than vibration.

Table I. Results of Female Choice Experiments.

Female	Competing Males	No. of Copulations	χ^2	Significance
PPS	PPS	17	8·05	1·0%
	PAC	25		
PAC	PPS	12		
	PAC	30		
PPS	PPS	23	4·25	5·0%
	PAL	24		
PAL	PPS	13		
	PAL	37		
PAC	PAC	20	—	—
	PAL	23		
PAL	PAC	23		
	PAL	19		

The reduced success of the small males allows us to put forward a hypothesis to explain why they exhibit more vibration than the control stock. It is possible that, within the small lines, there has been competition between males and thus selection for increased vibration which would tend to compensate for the otherwise deficient courtship.

Selection Effect II

To test this hypothesis, flies were selected for large and small body size in exactly the same manner as before but instead of placing all ten selected pairs of each line in stock bottles each pair was introduced separately into a culture vial. Under these conditions there could be no selection pressure for increased vibration.

Results

The courtship of fifteen males from the small (PVS), large (PVL), and control (PVC) lines thus set up was examined each generation. Fig. 8 is a graph of generation plotted against deviation of percentage vibration from control. On the hypothesis presented it would be expected that there would be no deviation from control in the amount of vibration in the small males'

courtship and this is what occurs. Thus the elimination of sexual competition between small males has also eliminated the divergence in courtship behaviour. The large (PVL) males' courtship has diverged in the same manner as in the mass culture large lines (PAL, PBL, PPL), the regression of PVL on PVC for percentage vibration being significant ($p<1{\cdot}0$ per cent.). This also is what would be expected. No difference in mating success was found between the original lines and control and therefore there was no reason to suspect that the divergence of courtship in the former was the result of selection.

The activity of these two selected lines was also measured and compared with the control. The large, PVL, males were found to be significantly less active than control ($P<1{\cdot}0$ per cent.) but there was not a comparable divergence of the small males.

Selection Effect III

As a further test of the hypothesis ten pairs of small, (PVS), flies were placed in a half-pint culture bottle and selection for small size was continued under mass mating conditions as in the original small selected lines (PAS, PBS, PPS). As a control ten pairs of PVC flies were also transferred to a culture bottle. The courtship of ten pairs of each was examined every alternate generation. Fig. 8 shows percentage vibration for this small line (SRS) expressed as deviation from control. The reintroduction of sexual competition between males in the small line has been followed by an increase in the average percentage vibration. This is significant at the 1·0 per cent. level.

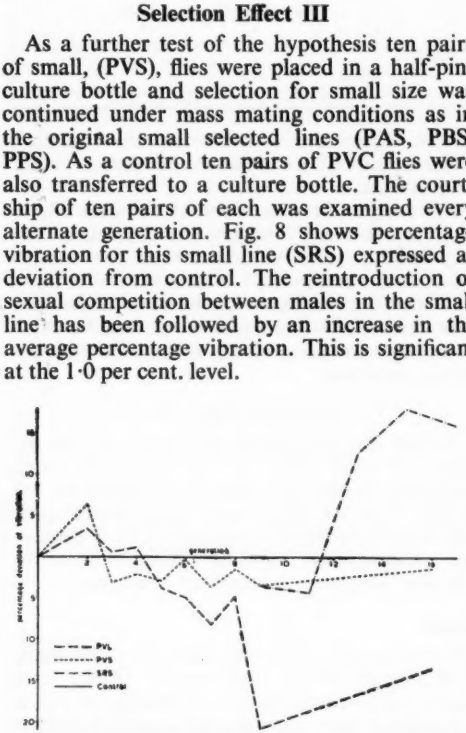


Fig. 8. Percentage deviation of vibration from control in flies subjected to two-way selection for body size but with sexual competition between males eliminated (PVL and PVS). Competition reintroduced at generation 9 in the small line results in increased vibration (SRS).

As an additional precaution the PVL, PVS and PVC lines were continued during this period and their courtship examined near the end of the experiment. Fig. 8 shows that the situation remains unchanged in them.

Discussion

Two important points emerge from these experiments. The first is that the seemingly comparable changes in courtship behaviour in the small and large selected lines on analysis proved to be the result of different causes. The second is the possible implications of these findings on the evolution of behaviour systems.

In the small selected lines the pattern of courtship behaviour was apparently changed by the action of a secondary selection pressure, proferring an advantage to flies that exhibited a high percentage of vibration in their courtship. This selection pressure arose as a result of decreased mating success following reduction in body size. The reasons for this reduction in success may be that the small flies, by virtue of their reduced body size and wing area, are less stimulating to the females. Inbreeding may also have a deleterious effect on courtship success as Smith (1956) has shown for *D. subobscura*, and one of the consequences of selecting for small body size is that the flies become inbred and this does not happen during selection in the opposite direction (Robertson, 1955).

In the large selected lines increased body size, reduced activity and low percentage vibration may be connected. Reduced activity seems more a product of large body size than of small as it occurred in the PVL line but not in PVS. However, it would be difficult to demonstrate with certainty that reduced activity in the large lines is definitely correlated with reduced vibration. A comparable argument to that stated above would explain why the large males, although exhibiting less of the sexually stimulating element, vibration, are equally successful in obtaining mates as the controls. Their increased body size and wing area would tend to compensate for this lowering of courtship "intensity."

The changes that have occurred in the courtship of the selected lines are similar to the differences that exist between related but sexually isolated species. The results of comparative ethology suggest that such species differ in their behaviour quantitatively rather than qualitatively. One of the differences in sexual behaviour between the sibling species, *Drosophila melano-*

gaster and *D. simulans*, as demonstrated by Manning (1959), is that courtship elements which are common to both differ in their frequency due probably to a change in their thresholds. Tinbergen (1959) and others working with gulls have shown that an overall similarity exists between the various species' reproductive behaviour. It seems that often a pool of existing behavioural elements has become modified from species to species in their frequency and importance. The example described in this paper might provide a model to explain how some behavioural isolating mechanisms have occurred in nature.

Summary

1. Lines of *Drosophila melanogaster* selected for large and small body size differ in their courtship. Small males have more and large males less vibration in their courtship than the controls.

2. Flies that were small due to environmental causes did not behave in the same manner as the small selected males.

3. No correlation was found between courtship and size in the F2 progeny crosses between large and small lines.

4. It was therefore concluded that the changes found in the courtship of the selected lines are not the inevitable result of increase and decrease in body size.

5. All the selected lines were less active than the controls. No connection between general activity and the differences in courtship can be postulated.

6. Small males are less successful in obtaining mates than the large or control males when in competition with them.

7. It is therefore suggested that the difference in the small males' courtship is due to selection pressure for increased amounts of vibration to counteract otherwise deficient courtship.

8. This was tested by selecting for large and small body size under conditions where competition between males was eliminated. As predicted no change occurred in the small males' courtship until sexual competition was reintroduced. The large males' courtship diverged as before, showing that changes in their courtship are not due to selection.

Acknowledgments

I am indebted to Dr. A. Manning for his guidance and help throughout the course of this work, to Dr. Margaret Manning for reading the manuscript and making many helpful criticisms, to Dr. F. W. Robertson who allowed me to use his selected stocks and for many useful discussions on the genetical aspects of the work and to Dr. L. J. Hale for his help with the statistical analyses.

REFERENCES

Bastock, M. (1956). A gene mutation that changes a behaviour pattern. *Evolution*, **10**, 421-439.

Bastock, M. & Manning, A. (1955). The courtship of *Drosophila melanogaster*. *Behaviour*, **8**, 85-111.

Manning, A. (1959). The sexual behaviour of two sibling Drosophila species. *Behaviour*, **15**, 123-145.

Maynard Smith, J. (1956). Fertility, mating behaviour and sexual selection in *Drosophila subobscura*. *J. Genet.*, **54**, 261-279.

Robertson, F. W. & Reeve, E. C. R. (1952). Studies in quantitative inheritance. 1. The effects of selection of wing and thorax length in *Drosophila melanogaster*. *J. Genet.*, **50**, 414-448.

Robertson, F. W. (1955). Selection response and the properties of genetic variation. *Cold Spr. Harb. Symp. quant. Biol.*, 166-177.

Sturtevant, A. H. (1915). Experiments on sex recognition and the problem of sexual selection in Drosophila. *J. anim. Behav.*, **5**, 351-366.

Tinbergen, N. (1959). Comparative studies of the behaviour of gulls (Laridae); a progress report. *Behaviour*, **15**, 1-70.

Accepted for publication 30*th August*, 1960.

VARIABILITY OF RESPONSE IN A DETERMINED TURNING SEQUENCE IN THE MEAL WORM *(Tenebrio molitor)*: AN EXPERIMENTAL TEST OF ALTERNATIVE HYPOTHESES

BY JOSEPH H. GROSSLIGHT* AND PAUL C. HARRISON
Department of Psychology, The Pennsylvania State University

A number of studies (Lepley & Rice, 1952), (Grosslight & Ticknor, 1953) have demonstrated that for paramecium and meal worms the probability of a turn in a particular direction at a T-choice point is a function of the direction of a previous forced turn (i.e. the organism will tend to turn in the opposite direction from the forced turn). The basis for this prediction was the Hullian principle of reactive inhibition. Jensen (1959) has raised a number of questions concerning the reactive inhibition explanation of the results. He reasons that the principle of centrifugal swing (Maier & Schneirla, 1935) along with the principle of thigmotaxis would account for the results. According to these principles the organism on the forced turn is carried to the outside wall of the alleyway by centrifugal swing. Having then been placed in this specific position the organism then guides along that side until contact is lost at the choice point. The turn then will be toward the guiding side in an apparent attempt to maintain contact. For example, if the forced turn is to the right then centrifugal swing takes the organism to the outside on that turn and consequently the left wall becomes the thigmotactic guide, leading, says Jensen (1959), to a left turn at the choice point. Jensen is supported in this analysis by the negative findings of Rice & Lawless (1957) on the flatworms, *Planaria dorotocephala*, in which thigmotactic influences were controlled by ignoring animals which guided along the side of the maze. One finding of the Grosslight & Ticknor (1953) study is overlooked in such an explanation of their results. They found that the probability of opposite turn decreased as a function of the distance from the forced turn. Why the effect of guiding on one side should decrease as a function of distance is not clear unless one speculates about some kind of adaptation or inhibition for thigmotaxis itself.

Although it may be impossible completely to eliminate the effects of thigmotaxis, except by a discard procedure, it is possible to control it by producing thigmotactic influences on both sides of the organism. A V-shaped alleyway would appear to accomplish this as the organism fits in it with *both sides* of his body in contact with the side walls. Further, the V-shaped maze should minimize centrifugal swing effects.

*The author wishes to thank the members of his class in Experimental Psychology for the actual execution of the research.

Method

Subjects: the subjects of this experiment were 766 meal worms, larvae of *Tenebrio molitor*. Although no measurement was made as to their length and width, all worms were selected for approximate fit into the V-shaped alleyways.

Apparatus: Four mazes (Fig. 1) were made of plaster of Paris, from moulds with V-shaped moulding as the imprint source. Each maze was carefully sanded with crocus cloth to remove any apparent irregularities and given a thin coat of beeswax to affect a smooth non-powdering alleyway. Preliminary tests indicated that the worms rolled to one side in the V-slot so that their legs were against one side wall and body against the other. In order to correct this characteristic, the bottom of the V-slot was flattened by drawing a screwdriver, 3 mm. wide, through the alleyway. The selection of animals that fitted, by inspection, into the groove still seemed to guarantee dual side contact in most cases. The four mazes were as follows:

1. R-T-3: a maze with a 4 cm. pathway leading to a forced right-turn (R), followed by a 3 cm. alleyway leading to a choice point (T).

2. L-T-3: the mirror image of the R-T-3 maze, i.e. forced left turn (L) followed by a 3 cm. alleyway to choice point (T).

3. R-T-6: a maze with a 4 cm. pathway leading to a forced right turn followed by a 6 cm. alleyway leading to choice point.

4. L-T-6: the mirror image of the R-T-6 maze, i.e. forced left turn followed by a 6 cm. alleyway to choice point.

Procedure: The meal worms were maintained in a growth mash of wheat bran and middlings

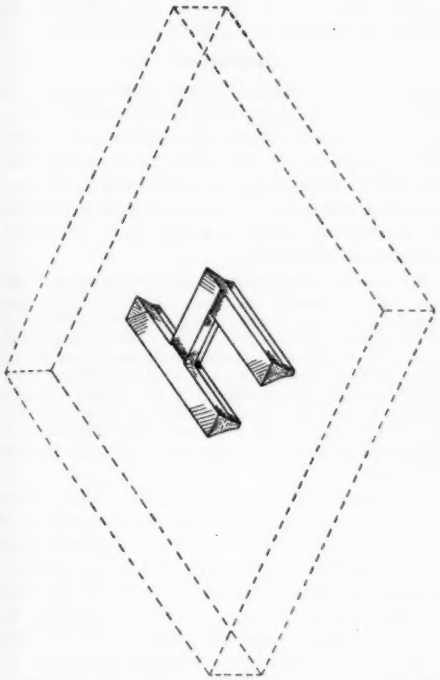


Fig. 1. Sample maze showing configuration of pathway.

and were sifted from it approximately 15 minutes before actual run. At this time they were placed in a large pyrex dish and exposed to a 60-watt electric light bulb. Exposure to light after being removed from the growth mash insured lively activity. Any larvae showing signs of pupating, moulting, general lethargy, or size inappropriate to the maze were discarded at once. Each maze was placed on a 5·5 in. × 6 in. platform on a levelled table tripod. This insured against any biasing effect of gravity in determining turns. A 150 watt protector flood light was suspended directly over the centre of the tripod in order to insure a uniform light field over the maze. To insure further against light-bias, an equal number of animals were run with the maze orientated in the four major quadrants. The quadrant order of running for each maze followed essentially the method of counterbalancing. The standard procedure and rules for the single run each worm made were as follows: the animal was placed by means of tweezers into the beginning of the 4 cm. alleyway and a glass cover was placed over the entire maze. One and one-half (1-½ cm.) from each turn and choice point a line was drawn so that any animal that rolled on its side from this point into the turn would be discarded. Any animal taking longer than 30 seconds to complete the run or more than 5 seconds to make a choice was discarded.

Results and Interpretations

In order to insure that the behaviour at the T-choice was not a function of bias in the alleyway prior to the choice or at the choice itself, a pre-test, treating each maze as a single T maze, was carried out. This was affected by placing the pretest animals in the alleyways beyond the forced turn, i.e. in the 3 cm. or 6 cm. alleyway leading to the T-choice. Two hundred and fifty-six* meal worms were employed in this pretest.

The prediction here is that without a forced turn in sequence, the right-left choice at the choice-point should not differ from a chance probability of 50-50. The results of this pretest (Table I) support a non-bias affect at the choice-point as none of the proportion of right-left choices differ significantly from 50-50.

Table I. Distribution of Turns in Pretest of Mazes and Test of Significance from 50:50.

Maze	Direction of Turn N	R%	N	L%	χ^{2*}
R-T-3	28	·44	36	·56	1·00
L-T-3	39	·54	33	·46	·50
R-T-6	27	·48	29	·52	·08
L-T-6	35	·54	29	·46	·50

*All χ^2 values fail to be significant even at the 0·3 level.

In the experiment proper, with thigmotaxis influences controlled and centrifugal swing minimized, the results support the previous findings of Grosslight & Ticknor (1953) on the effect of determined turn sequence on subsequent choice. Forcing an animal in one direction, either right or left, increases the probability of subsequent choice to be in the direction opposite to the forced turn. Based on an expected frequency of 50 per cent. of total turns right (left), a chi-square was computed for each maze. Deviation from the expected value was significant at or

*Due to a restriction on the number of worms available for this pre-test and failure of two of the students to collect some of this data, the number of worms tested in all four mazes is not equal.

beyond the ·01 level of significance for three mazes. Deviation for the fourth maze (R-T-6) is just short of significance at the ·05 level (Table II).

Table II. Number and Proportion Turning in Predicted Direction for All Mazes.

Maze	Total N	Number in Predicted Direction	% in Predicted Direction	χ^2
R-T-3	128	104	81	50·00**
L-T-3	128	108	84	60·50**
R-T-6	128	75	58	3·78
L-T-6	128	93	73	26·28**

**Significant at ·01 level with 1 d.f.

The combination* of mirror images into one overall proportion for predicted turn further clarifies the major results of this study. The behaviour of the animals, at a choice point, with thigmotaxis influence controlled, is influenced by the direction of the preceding turn. Further, the magnitude of this effect decreases as the distance between the forced turn and the choice-point is increased. (Table III).

Table III. Combined Percentage Turning in Predicted Direction as a Function of Distance from Preceding Choice.

Maze	N	% turning in Predicted Direction	χ^2 from 50-50
R-T, L-T } 3 cm	256	83	110·25**
R-T, L-T } 6 cm	256	66	25·00**

**Significant beyond ·01 level of confidence with 1 d.f.

Further, the magnitude of the turning response in the predicted direction decreases as the distance from the forced turn is increased. The difference between the 83 per cent. for the 3 cm. mazes (combined) and 66 per cent. for the 6 cm. mazes is significant beyond the ·01 level of confidence (t=8·89). These percentages are very close to the percentages found (3 cm=84 per cent. and 6 cm.=75 per cent.) in the original Grosslight & Ticknor (1953) study.

*Some risk in combining mirror images exists as a significant difference occurred between R-T-6 and L-T-6 (t=4·74). However, the difference between R-T-3 and L-T-3 is not significant.

Discussion

The nature (characteristic) of a response, as well as its probability of occurrence, in relation to prior response events, are matters of considerable importance in our attempts to understand behaviour. One possible relationship between preceding and subsequent responses is covered by the concept of reactive inhibition (response-produced inhibition).

"When any reaction occurs, the probability of its later occurrence is reduced. The probability of its later ocurrence increases with the continuing succession of following, dissimilar reactions. It is proposed that the probability of later occurrence would be reduced progressively with continued repetition; and that the degree of reduction would be proportional to the degree of repetitiousness. It is further proposed that this reduction in the probability of occurrence for a particular reaction would enhance the probability of occurrence for other reactions in the repertoire. (Lepley & Rice, 1952)."

Considerable research (Prachtl, 1953), (Glanzer, 1953), has demonstrated the limitations of response-produced inhibition as a concept which makes variability of behaviour a lawful product of behaviour itself. However, it would be naive to assume that changes in the relationship between responses were the product of a single variable and, although, response-produced inhibition is limited, it is not to be discarded altogether at this time. The results of this study which show a clear relationship between a turning response at a choice-point as a function of an earlier forced choice is consistent with the reactive inhibition hypothesis. Because of the controls exercised in this study, interpretations in terms of the alternative hypotheses of centrifugal swing and thigmotaxis appear untenable.

Summary

This study attempts to control thigmotaxis and centrifugal swing as the basic factor in the alternation behaviour of the meal worm, larvae of *Tenebrio molitor*. In order to eliminate these variables, alleyways of the mazes were essentially V-shaped in construction. As a result, centrifugal swing to one side or another is substantially reduced and since the construction of the maze guarantees contact on both sides of the organisms' body, thigmotaxis control in determining turning behaviour is eliminated.

Four mazes were employed in this study. Two of the mazes had a 3 cm. alleyway from forced turn to T-choice. These mazes were mirror images of each other; the direction of forced turn

being right for one and left for the other. Two of the mazes had a 6 cm. alleyway from forced turn to T-choice. These mazes were mirror images of each other. All mazes were pre-tested for bias by using only the T portion of the maze. The distribution of right and left turns in the pre-test for all mazes did not differ significantly from chance.

In the basic study, 512 meal worms were employed with N=128 for each maze. In both the 3 cm. and 6 cm. maze (combined mirror image), the tendency to turn in the opposite direction from the forced turn was highly significant. The magnitude of the effect decreases significantly from the 3 cm. to the 6 cm. maze.

These findings duplicate the original findings of Grosslight & Ticknor (1953). The results in relation to the concepts of reactive inhibition, the original hypothesis, and the alternate explanations of centrifugal swing and thigmotaxis are discussed.

REFERENCES

Glanzer, M. (1953). The role of stimulus satiation in spontaneous alternation. *J. exp. Psychol.*, **45**, 387-393.

Grosslight, J. H. & Ticknor, W. (1953). Variability and reactive inhibition in the meal worm as a function of determined turning sequence. *J. comp. physiol. Psychol.*, **46**, 1, 35-38.

Jensen, D. D. (1959). A theory of the behavior of *Paramecium aurelia* and behavioral effects of feeding, fission, and ultraviolet microbeam irradiation. *Behaviour*, **15**, 1-2, 82-122.

Lepley, W. M. & Rice, G. E. (1952). Behavior variability in paramecia as a function of guided act sequences. *J. comp. physiol. Psychol.*, **45**, 283-286.

Maier, N. R. F. & Schneirla, T. C. (1935). *Principles of animal psychology*. New York: McGraw-Hill.

Prachtl, H. F. R. (1953). Zur Physiologie der angeboren auslösenden mechanism. *Behaviour*, **5**, 32-50.

Rice, G. F. & Lawless, R. H. (1957). Behaviour variability and reactive inhibition in maze behaviour of *Planaria dorotocephala*. *J. comp. physiol. Psychol.*, **50**, 105-108.

Accepted for publication 26th September, 1960.

BRIEF COMMUNICATIONS

BEHAVIOUR OF SOME HYBRIDS IN THE MALLARD GROUP *

By A. OGDEN RAMSAY
McDonogh School, McDonogh, Maryland

The inheritance of behaviour patterns presents an opportunity to understand the origin of behaviour and also to determine the innate aspects of behaviour. The technic of hybridization allows observations on these topics. Naturally only closed related forms will produce viable young and thus only some behaviour patterns can be observed.

Three species of surface-feeding ducks that had homologous displays were crossed. The species used were the Mallard (*Anas platyhynchos*), the Black Duck (*Anas rubripes*), and the Florida Duck (*Anas fulvigula*). The males of these species showed the following displays as named and described by Konrad Z. Lorenz (1958). The Evolution of Behaviour, Scientific American, 199 (6): 67-78): (1) Bill-shake, (2) Head-flick, (3) Tail-shake, (4) Grunt-whistle, (5) Head-up-tail-up, (6) Turn-toward female, (7) Nod-swimming, (8) Turning-back-of-head, (9) Bridling, (10) Down-up. (See Fig. 1). The sequence as well as the movements are similar in the different species. However, the Florida duck did not show the down-up movement and was more apt in isolation to give such movements as the grunt-whistle. The Black Duck sometimes gives nod-swimming movement without the head-up-tail-up display. Typical sequences for all three species were tail-shake, bill-shake, head-flick (3-1-2); tail-shake, bill-shake, grunt-whistle (3-1-4); bill-shake, down-up (1-10); bridling' nod-swimming (9-7) (post-copulatory display); bill-shaking, head-up-tail-up, turn toward female, nod-swimming, turn-back-of-head (1-5-6-7-8). A complete series of displays would be 3-2-3-1-4-3-5-6-7-9 (Lorenz).

A male hybrid between a male Black Duck and a female Mallard never gave the nod-swimming (7) following the head-up-tail-up (5) display. In the Mallard this display is omitted only 7 per cent. of the time and in the Black Duck 20 per cent. of the time in the typical sequence. These percentages are based on approximately 75 recorded observations for each animal. In this hybrid, as in the others studied, the sequence of movements, -bill-shaking (1), grunt-whistle (4)- is reversed. Sometimes in the parent species this sequence is tail-shaking (3), bill-shaking (1), grunt-whistle (4). In the hybrid this is reversed to grunt-whistle, tail-shaking, bill-shaking (3-1-4) changed to 4-3-1). This hybrid also showed other occasional deviations from pattern such as head-up-tail-up, down-up (5-10). These occasional deviations are never found in the parent species.

The second male hybrid (Black Duck male and a Florida Duck female) showed a similar deviation from sequence. This hybrid gave the sequence grunt-whistle, tail-shaking (4-3), rather than the sequence tail-shaking, bill-shaking, grunt-whistle (3-1-4). It also showed some occasional changes in sequence such as head-up-tail-up, down-up (5-10). These sequences are characteristic of neither parent species. It also occasionally repeated some of its displays such as 5-6-7-5-6-7. Neither of the parent species showed this tendency.

A third male hybrid, (Mallard and the male Pintail (*Anas acuta*), was also studied. The Pintail has similar displays to the other species but the sequences are different. This hybrid gave the down-up movement before the head-up-tail-up display (10-5-1), whereas in the Pintail the down-up movement is linked to the grunt-whistle (4-10), and in the Mallard to the bill-shaking (1-10). Also, in this hybrid the grunt-whistle was given abruptly and then followed by the "preliminary" movements (4-3-1) rather than (3-1-4).

It seems significant that in all 3 hybrids the grunt-whistle is given abruptly and then followed by one or more of the "preliminary movements." Characteristically (4-3-1) rather than (1-3-4); sometimes (4-1) rather than (1-4), or (4-3) rather than (1-3-4). These observations suggest that, although the pattern is inherited, the sequence in hybrids is either inherited in an aberrant form or some failure of learning occurs.

*Accepted for publication 14th September, 1960.

*The work described in this paper was supported in part by Grant M-776 of the National Institutes of Health, Public Health Services, Department of Health, Education, and Welfare, Bethesda, Md. The grant is under the direction of Eckhard H. Hess. The author would like to thank Mr. E. Carey Kenney of the McDonogh School for preparing the illustrations.

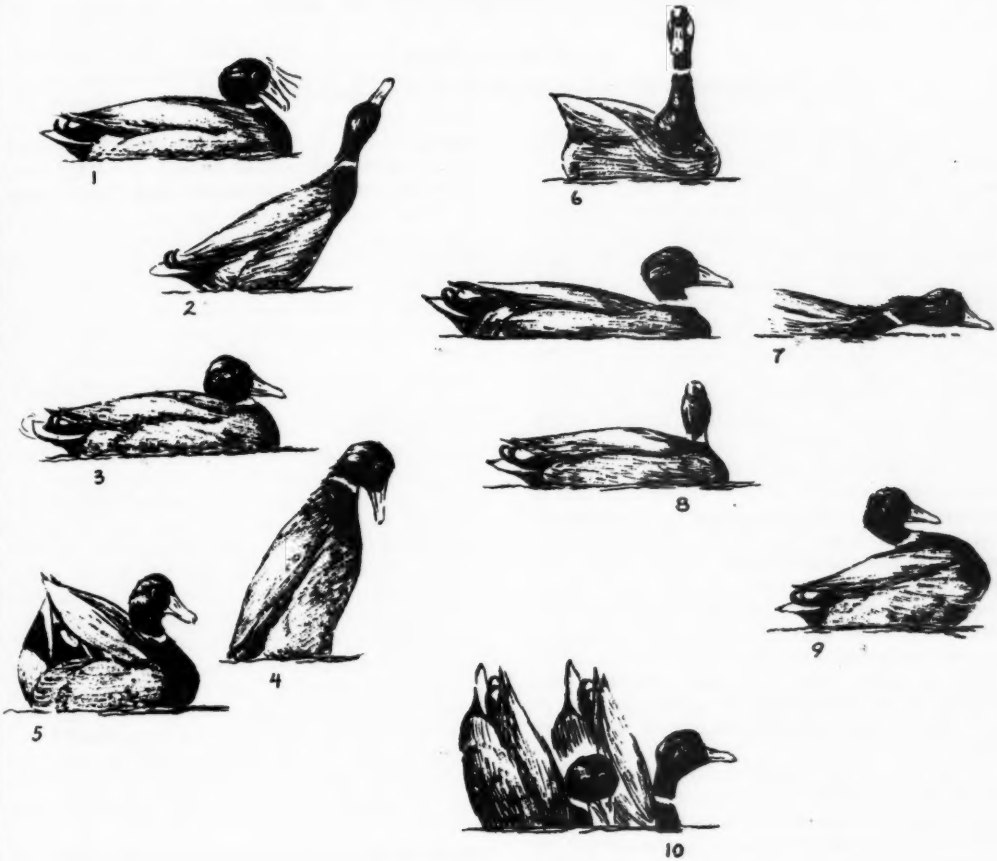


Fig. 1. Types of display.
(1) Bill-shake, (2) head-flick, (3) tail-shake, (4) grunt-whistle, (5) head-up-tail-up, (6) turn toward female (7) nod-swimming, (8) turning-back-to-head, (9) bridling, (10) down-up.
(redrawn after Rudolf Freund in *Scientific American*, 199, 67-78).

INTERTIDAL TERRITORY IN FISH

By D. B. CARLISLE

Marine Biological Association of the United Kingdom, Plymouth

Amongst coastal and freshwater fish, territory-holding during the reproductive state is common. Amongst marine fish, we may cite the black bream, *Spondyliosoma cantharus* (Gmelin). The male constructs and defends a nesting site, attacking and driving away males of the same species, other fish, crustaceans and any animals which invade the area surrounding the nest. He may even pull a lobster off the nest by seizing it by the antenna (Wilson, 1958), or push it from behind with vigorous swimming movements. Territorial behaviour in fish outside the breeding season is, however, less well documented, if by "territory" we mean a defended area. Many fish may take up definite stations on streambeds, crannies in rocks or even corners in aquarium tanks, but, in contrast to the abundant literature on birds (see Hinde, 1956), I am unaware of any account which would imply that non-breeding marine fish defend such areas (see also Thorpe, 1956, p. 267 footnote). Even the hierarchical station-holding by trout in a stream, in many ways so reminiscent of peck-order amongst hens, has only recently been shown to be maintained by active defence or territorial display (Kalleberg, 1958) in captive fish.

This state of affairs may reflect an actual lack of territorial defence by non-breeding fish or, more likely, it may result from the difficulty of observation under water. With the advent of underwater swimming, this difficulty disappears. During the summer of 1959 I spent many hours observing fish around an intertidal reef on the South Coast of Devon (50°16′ N., 3°52′ W.). The vertical intertidal distance here varies from 2 m at neap tides to 6 m at spring tides. The reef extends from the low cliffs to about mid-tide level and is intersected with sandy-bottomed gullies (see Fig. 1), whilst the rocks themselves are covered by weed, mainly the green *Enteromorpha* and the brown wracks, *Fucus* spp. I spent some time on this reef, during the daytime, when the tide was up, on two or three days a week, throughout a period of 3½ months from the end of May until early September. No observations were made at night. It soon became possible to recognize individual fish by markings, damaged fins and scars, so that it was apparent that the area was in general occupied by the same individuals, namely two large bass, *Morone labrax* (Linnaeus) and seven grey

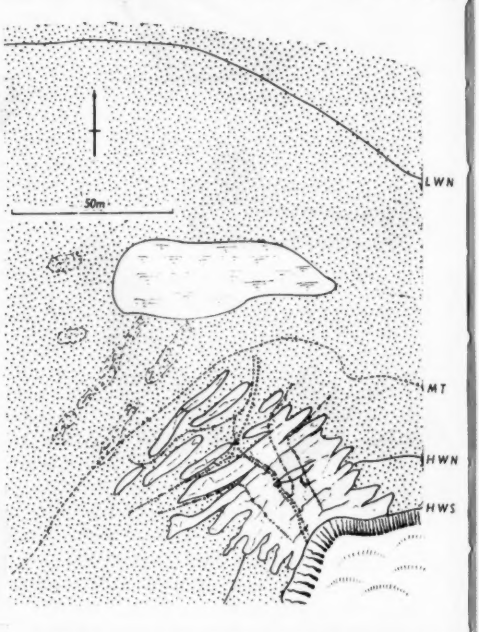


Fig. 1. Sketch map of the reef and surrounding areas. The sands shift at every tide and some of the off-lying rocks are more often than not under the sand; the pool changes shape at each tide for the same reason, but was approximately as shown for most of the summer of 1959.

. . . . . approximate limits of the bass territories;

·· – ·· – ·· – ·· approximate limits of the mullet territories;

H W N, high-water mark of neap tides;

H W S, high-water mark of spring tides;

L W N, low-water mark of neap tides;

M T, mid-tide level.

mullet, *Mugil labrosus* Risso, of about average size. Provided one made no abrupt movement it was possible to approach them quite closely and by lying still on the surface and looking down they could be seen feeding undisturbed.

The fish arrived with the rising tide as soon as the water was deep enough for them to swim—

some 15-20 cm. They came in even when the water was rough enough to be dangerous to the observer. Under these conditions they travelled in the waves and seemed to risk stranding on uncovered parts of the reef. The bass came in and left individually. When the water was calm enough to observe this point the mullet arrived and left in a school. Both species stayed until about an hour after high tide, swimming off when there was still plenty of water over the reef, but as soon as the tide began to run strongly. Each fish when on the reef kept to a definite area, indicated on the sketch map. The areas occupied by the mullet came within those of the bass, but the two species never seemed to take any notice of one another.

The two bass rarely encroached on each other's areas and if they were disturbed the flight line avoided the area held by the other fish. When undisturbed they lurked in gullies and around waving fronds of the larger brown algae, pouncing out upon passing sand eels or diving towards the sand storms sent up by shrimps. During the feeding dart the mouth was almost closed until the last moment and the anal and dorsal fins were folded down until erected in the moment of seizing the prey, when they were used for manoeuvre and braking. It is well-known that the stream-lined fish swim faster in a straight line when all the fins are folded back; in normal swimming the fins are used only for manœuvre and braking. If a strange bass entered its territory the resident bass attacked. This attacking rush was quite different from the feeding dart: the dorsal and anal fins remained erect throughout and the mouth wide open. The attacker often attempted to bite the intruder by the caudal peduncle or elsewhere, but usually the latter turned tail and fled, dodging the bite. The most vicious attacks were made when a resident bass, cruising slowly round one of the larger rocks of the reef, came face to face with an intruder which was already well within the territory. Pursuit always took the fish beyond my limit of vision and outside the area of the reef. I never saw an intruder bite back, but this may have been because all the bass which approached were considerably smaller than the two residents. Once the intruder had turned tail, the attacker's fins were folded down, the mouth closed and the pursuer adopted a more efficient swimming posture.

The mullet browsed on the green algae of the reef, but if they were disturbed they immediately schooled and territorial boundaries were ignored. If another mullet approached when they were quietly feeding within their territories all the mullet in sight ceased feeding. Any incursion within a territory was met by the resident fish rushing towards the intruder with mouth agape, halting with fins spread and then making a further rushing approach. One or two such rushes were sufficient to drive a smaller intruder away, but on the few occasions when an intruder was larger than the resident, a series of such rushing approaches succeeded in driving off the intruder without any actual contact between the fish. The mullet did not chase an intruder more than about 5 m outside the territory.

Here, then, are examples of active defence of non-breeding territories in two species of fish. It is noteworthy that the territories of the bass overlapped those of the mullet but that each species only defended the territory against intruders of the same species. I did not, however, observe attempted intrusions by any other large fish species. These intertidal feeding territories were only occupied for part of the day and during their defence the fish showed specific patterns of behaviour. Fins in particular were erected in ways not seen for other types of swimming motion and were presumably used to threaten the intruder and to make the defender appear more alarming to the intruding fish.

REFERENCES

Hinde, R. A. (1956). The biological significance of the territories of birds. *Ibis*, **98**, 340-369.

Kalleberg, H. (1958). Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *Salmo trutta* L.). *Rep. Inst. Freshw. Res. Drottning.*, **39**, 55-98.

Thorpe, W. H. (1956). *Learning and instinct in animals.* London: Methuen.

Wilson, D. P. (1958). Notes from the Plymouth aquarium. III. The breeding of *Spondyliosoma cantharus* (Gmelin). *J. mar. biol. Ass. U.K.*, **37**, 299-304.

Accepted for publication 15*th June*, 1960.

THE BEHAVIOUR OF FREE-LIVING MITES AS AFFECTED BY HUMIDITY

(Acarina; Oribatoidea)

By D. S. MADGE

Department of Entomology, Rothamsted Experimental Station, Harpenden, Herts.

Oribatid mites may be divided into groups of "indicator species" (ecotypes) as follows: xerophyl, mesophyl or hygrophyl. The experiments outlined here were made to study the effects of humidity on mites from these groups.

Mites were exposed in a linear humidity chamber made of glass with a sintered glass floor. Most experiments were done at 15°C. in the dark and records were taken half-hourly or hourly for 3-4 days.

Humerobates rostrolamellatus (a xerophyl) much preferred the lowest humidity but this initial dry reaction was reversed to a moist one over 4 days. For instance, 34 per cent. and 9 per cent. of them chose 10 per cent. and 95 per cent. R.H. respectively for 1-12 hours but from 91-96 hours 16 per cent. and 20 per cent. had selected the same humidities. Both adult and juvenile *Belba geniculosa* (a mesophyl) chose the highest R.H. region after a day. *Platynothrus peltifer* (a mesophyl or a hygrophyl) also chose the moist zone. Adult *Fuscozetes fuscipes* (a hygrophyl) did not react to linear humidities.

To eliminate end-effects experiments were also done in a "bifacial humidity gradient" and these confirmed the above results. Desiccated mites chose their preferred humidities quicker than normal mites. For example, 73 per cent. desiccated adult *B. geniculosa* chose 95 per cent. R.H. during 0-3½ hours whereas only 36 per cent. normal mites selected the same region. The initial dry reaction of *H. rostrolamellatus* was, however, not immediately reversed even after 4 days desiccation. Experiments at 5°C. or 25°C. and tests on starving mites did not change the preferred humidities of the mites.

An alternative humidity chamber was made from paraffin wax cells with perspex sides and a sintered glass floor. Results confirmed the results given above, but gave some additional information. Batches of *H. rostrolamellatus* reacted differently to a choice of 30 or 95 per cent. R.H., depending upon their initial distribution. *B. geniculosa* and *P. peltifer* showed greater sensitivity in the higher range of humidities rather than in the lower range. Results were again inconclusive with *F. fuscipes* and they appeared indifferent to any alternative humidity but possibly sometimes chose the moister humidity. With all the mites, the greater the differences of R.H. offered, the stronger is the humidity reaction. It was tentatively concluded that the hygroreceptors of *H. rostrolamellatus* function at all humidities, those of *B. geniculosa* and *P. peltifer* work at high humidities rather than at low humidities. Results with *F. fuscipes* suggest that this mite may have no humidity receptors.

A film showing the behaviour of individual *B. geniculosa* in a humidity gradient suggested that the hygroreceptors might be located on the forelegs. This was supported by laboratory experiments.

PROCEEDINGS OF THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

A meeting of the Association was held on 15th and 16th December in the Psychology Department, Birkbeck College, London, by kind permission of Professor C. A. Mace. The President, Dr. K. Mellanby, C.B.E., was in the chair.

Thursday, 15th December

THE EFFECTS OF CHEMICALS AND DRUGS ON BEHAVIOUR

USING DRUGS TO STUDY ANIMAL BEHAVIOUR. A REVIEW. By HANNAH STEINBERG (*London*) *

Research on the relations between drugs and animal behaviour has much increased during the last ten years: for example, a recent bibliography (Caldwell, 1958) lists 2 animal studies with chlorpromazine in 1953 and 44 in 1956. Many new drugs which act on the nervous system have been introduced, and this has also stimulated interest in older drugs like barbiturates; and many kinds of animal and of behaviour have been studied.

Most investigations can be roughly classified according to their predominant aim, and in practice each is apt be to pursued by workers with different backgrounds: either (i) behaviour is used to analyse the action of drugs, or (ii) drugs are used as tools to analyse behaviour. The two aims are of course complementary, since a better understanding of the mode of action of these drugs partly depends on a better understanding of behaviour, and vice versa.

(i) Drugs do not usually act exclusively on any one kind of behaviour. But if several doses of the same drug are used, it can sometimes be shown that one kind of behaviour is modified by a lower dose than some other kinds; 'profiles' can be plotted for each drug showing the doses at which different kinds of behaviour become sensitive to its effects, and in this way striking quantitative differences between the patterns of action of different drugs can be demonstrated, e.g. Janssen (in the Press). Systematic information of this sort is most easily obtained when relatively quick and simple tests of behaviour are used, as in 'screening' new compounds, but the more information becomes available the more it will help those who want to use drugs as tools for analysing more complex kinds of behaviour step by step. (ii) Anaesthetics and curare have long been found valuable for elucidating the physiological bases of learning and memory, drugs like amphetamine and 'tranquillizers' are being much used to study motivation and emotional behaviour in rats, cats and monkeys (see e.g. Miller & Barry, 1960), and there are many other examples. Doses may again be crucial. Thus barbiturates—like alcohol—normally depress most forms of activity, but sometimes they stimulate it when given in small doses; whether they do this in a particular case will depend on the kind of activity, on the environment and on the past experience of the animal. It is possible that there are optimal doses for demonstrating effects of environment and experience.

*The preparation of this review and of the list of publications was supported by research grant MY-3313 from the National Institute of Mental Health, Public Health Service, U.S.A.

REFERENCES

Caldwell, A. E. (1958). *Psychopharmaca.* Washington: U.S. Dept. Health, Education & Welfare.

Janssen, P. Pharmacology of R.1625, including a review of methods of testing for the action of drugs on the nervous sytem. In *Symposium on R.*1625, *Haloperidol.* (In the Press).

Miller, N. E. & Barry, H. (1960). Motivational effects of drugs. *Psycho-pharmacologia,* **1,** 169-199.

SOME PUBLICATIONS RELEVANT TO THE EFFECTS OF DRUGS ON ANIMAL BEHAVIOUR *
By HANNAH STEINBERG & CHRISTINE TINSON (*London*)

1. SYMPOSIA AND BOOKS.

Ann. N.Y. Acad. Sci. (1954) **59,** 1-140. Reserpine (Serpasil) and other alkaloids of Rauwolfia Serpentina: chemistry, pharmacology, and clinical applications.

Ann. N.Y. Acad. Sci. (1955). **61,** 1-280. Reserpine in the treatment of neuro-psychiatric, neurological and related clinical problems.

Ann. N.Y. Acad. Sci. (1956), **64,** 463-731. Experimental methods for the evaluation of drugs in various disease states; part 5, 630-731. Disorders of the central nervous system.

Ann. N.Y. Acad. Sci. (1956), **65,** 247-356. Techniques for the study of behavioral effects of drugs.

Ann. N.Y. Acad. Sci. (1957). **66,** 417-840. The pharmacology of psychotomimetic and psychotherapeutic drugs.

Ann. N.Y. Acad. Sci. (1957), **67,** 671-894. Meprobamate and other agents used in mental disturbances.

Ann. N.Y. Acad. Sci. (1959), **80,** 551-1045. Amine oxidase inhibitors.

Braceland, F. J. (ed.), (1959). *The effect of pharmacologic agents on the nervous system.* Baltimore: Williams & Wilkins.

Bradley, P. B., Deniker, P. & Radouco-Thomas, C. (eds.), (1959). *Neuro-psychopharmacology.* Amsterdam: Elsevier.

Brill, H. (intro. by), (1958). *Trifluoperazine: clinicial and pharmacological aspects.* Philadelphia: Lea & Febiger; London: Kimpton.

Caldwell, A. E. (1958). *Psychopharmaca.* A bibliography of psychopharmacology, 1952-57. Washington: U.S. Dept. Health, Education & Welfare.

Cholden, L. (ed.), (1956). *Lysergic acid diethylamide and mescaline in experimental psychiatry,* New York: Grune & Stratton.

Cole, J. O. & Gerard, R. W. (eds.), (1959). *Psychopharmacology.* Problems in evaluation. Washington: Nat. Acad. Sci.

Fields, W. S. (ed.), (1957). *Brain mechanisms and drug action.* Springfield: Thomas.

Featherstone, R. M. & Simon, A. (eds.), (1959). *A pharmacologic approach to the study of the mind.* Springfield: Thomas.

Garattini, S. & Ghetti, V. (eds.), (1957). *Psychotropic drugs.* Amsterdam: Elsevier.

Grebe, R. M. (ed.), (1959). Tranquilizers. Vol. 4 of *Handbook of toxicology.* Philadelphia: Saunders.

Harlow, H. F. & Woolsey, C. N. (eds.), (1958). *Biological and biochemical bases of behavior.* Madison: Univ. Wisconsin Press.

Himwich, H. E. (ed.), (1957). *Alcoholism.* Washington: Amer. Assoc. Adv. Sci.

Himwich, H. E. (ed.), (1957). *Tranquilizing drugs.* Washington: Amer. Assoc. Adv. Sci.

Hoagland, H. (ed.), (1957). *Hormones, brain function and behavior.* New York: Acad. Press.

Kline, N. S. (ed.), (1959). *Psychopharmacology frontiers.* London: Churchill.

Leake, C. D. (1958). *The Amphetamines.* Springfield: Thomas.

Lewis, G. P. (ed.), (1958). 5-*Hydroxytyptamine.* London: Pergamon.

Josiah Macy, Jr. Foundation; Abramson, H. A. (ed.). *Neuropharmacology.*
Transactions of the first conference, 1954, *New York,* 1955.
Transactions of the second conference, 1955, *New York,* 1956.
Transactions of the third conference, 1956, *New York,* 1957.
Transactions of the fourth conference, 1957, *New York,* 1959.
Transactions of the fifth conference, 1959, *New York,* 1960.

McIlwain, H. (1957). *Chemotherapy and the central nervous system.* London: Churchill.

Masserman, J. H. (ed.), (1959). *Biological psychiatry.* New York: Grune & Stratton.

Pennes, H. (ed.), (1958). *Psychopharmacology.* Pharmacologic effects on behavior. New York: Hoeber-Harper.

Richter, D. (ed.), (1957). *Metabolism of the nervous system.* London: Pergamon.

Rinkel, M. & Denber, H. C. B. (eds.), (1958). *Chemical concepts of psychosis.* New York: McDowell, Obolensky.

*Symposium on R.*1625, *Haloperidol, held at the Royal Society of Medicine on* 22*nd June,* 1960 (in the press).

Symposium on sedative and hypnotic drugs, 1954. Baltimore: Williams & Wilkins.

Uhr, L. & Miller, J. G. (eds.), (1960). *Drugs and behavior.* New York: Wiley.

Waelsch, H. (ed.), (1955). *Biochemistry of the developing nervous system.* New York: Acad. Press.

Wikler, A. (1957). *The relation of psychiatry to pharmacology.* Baltimore: Williams & Wilkins.

II. REVIEWS PUBLISHED IN JOURNALS, REPORTS, ETC.

Dews, P. B. (1958). Psychopharmacology. In Drill, V.A., *Pharmacology in Medicine.* New York: McGraw-Hill.

Feldberg, W. (1958). A physiological approach to the problem of general anaesthesia and of loss of consciousness. *Brit. med. J.,* **ii,** 771-782.

Gaddum, J. H. Antagonisms between drugs. In *Proceedings of the Second International Congress of Neuro-psychopharmacology.* (In the Press).

Jacobsen, E. (1959). The comparative pharmacology of some psychotropic drugs. *Bull. Wld. Hlth. Org.,* **21,** 411-493.

Kety, S. S. (1959). Biochemical theories of schizophrenia. Parts I and II. *Science,* **129,** 1528-1532 and 1590-1596.

Laurence, D. R. & Pond, D. A. (1958). The trade in tranquility. *Brit. med. J.,* **i,** 700-702.

Miller, N. E. (1958). Central stimulation and other new approaches to motivation and reward. *Amer. Psychol.,* **13,** 100-108.

Miller, N. E. & Barry, H. (1960). Motivational effects of drugs: methods which illustrate some general problems in psychopharmacology. *Psychopharmacologia,* **1,** 169-199.

Plotnikoff, N., Birzis, L., Mitoma, C., Otis, L., Weiss, B. & Laties, V. (1960). *Drug enhancement of performance.* Final report. Menlo Park, Calif.: Stanford Research Institute.

Riley, H. & Spinks, A. (1958). Biological assessment of tranquillisers. Parts I and II. *J. Pharm., Lond.,* **10,** 657-671 and 721-740.

Ross, S. & Cole, J. O. (1960). *Psychopharmacology. Ann. Rev. Psychol.,* **11,** 415-438.

Russell, R. W. (1960). An approach to the development of animal screening techniques in psychopharmacology. *Psychopharmacol. Service Center Bull.,* 1-7.

Russell, R. W. (1958). Effects of 'biochemical lesions' on behavior. *Acta psychol., Hague,* **14,** 281-294.

Schuster, C. R. (1959). A review of animal experimentation in psychopharmacology for the years 1900-1953. *University of Maryland Laboratory of Psychopharmacology Technical Report No.* 59-11.

Sidman, M. (1959). Behavioral pharmacology. *Psychopharmacologia,* **1,** 1-19.

Vogt, M. (1958). Pharmacology of tranqillizing drugs. *Brit. med. J.,* **ii,** 965-967.

Wikler, A. (1950). Sites and mechanisms of action of morphine and related drugs in the central nervous system. *Pharmacol. Rev.,* **2,** 435-506.

AN INTERDISCIPLINARY APPROACH TO THE STUDY OF CENTRAL NERVOUS FUNCTION. By P. B. BRADLEY (*Birmingham*)

A great variety of techniques and methods contributes to the analysis of central nervous function. Whilst the correlation of experimental results from different disciplines enhances their interpretation, it is only in terms of behaviour that we can determine the full functional significance of disturbances produced by lesions, electrical stimulation, the injection of drugs and changes in metabolism.

In electrophysiological studies of the effects of drugs on the brain, correlation of the results with behavioural changes is of prime importance. This is illustrated by the 'pharmacological dissociation' produced by certain drugs whose action is related to cholinergic mechanisms in the brain, in which the normal correlation between electrocortical activity and behavioural state of wakefulness and sleep is disturbed.

In other experiments, the effects of tranquillizers and hallucinogenic drugs have been shown to modify sensory influences feeding into the brain stem reticular formation which, through its ascending influences, is known to control levels of wakefulness and sleep. The use of conditioning techniques in studies of the effects of these drugs on thresholds for arousal produced by sensory stimulation has demonstrated the existence of a close relationship between the effects of the drugs and the neurophysiological mechanisms of conditioning and habituation. Thus LSD 25, a hallucinogenic drug, simulated the effect of positive conditioning of the arousal response to sensory stimuli and the tranquilliser chlorpromazine produced effects closely resembling habituation. Further experiments are in progress to analyse these mechanisms more fully.

PROBLEMS OF INTERPETING DRUG-BEHAVIOUR EXPERIMENTS. By R. H. J. WATSON (*London*)

The interpetation of Drug-Behaviour experiments will be influenced by whether you are using the behaviour to study the drug, or whether you are using the drug as a tool to investigate behaviour. In either case additional problems are found which involve the interpretation of the *particular* behaviour studied. This is particularly true in those cases where it is hoped to use a form of behaviour analogous to human behaviour, for example, investigating how tranquillizers reduce anxiety.

It cannot be assumed that similar behaviour is necessarily mediated by similar nervous mechanisms, and the importance of this in drug studies will be illustrated. Differences not only between species, but between strains of the same species have been shown to be critical in certain types of drug study. Tolerance for a drug may also depend on the state of the organism at the time of experiment, for example, daily metabolic rhythm, conditions of husbandry. The size of dose used may also give confusing results. It is well known that very small doses often produce effects opposite to those of larger doses, and these small doses are those best for behaviour studies.

The problem of side effects and multiple effects whilst in human therapeutics is largely a practical problem becomes, in animal studies, a major concern from the theoretical point of view, The change in behaviour may well be due to some side action of the drug rather than its main effect. It is suggested that drug-behaviour studies need a far more sophisticated experimental design that is usual at present.

THE TOXIC AND BEHAVIOURAL EFFECTS OF RESERPINE ON CATS. By W. A. BERESFORD, J. C. COLE & P. GLEES (*Oxford*)

Large doses of reserpine given to cats induce physiological and behavioural changes similar to those seen in monkeys but differing in degree and persistence. 2·5 mg/kg of reserpine was given intramuscularly to adult cats once or once daily for 5 days. Symptoms seen in cat and monkey are: 1. Those consistent with an altered sympathetic balance, e.g. salivation,

2. A motor impairment similar to Parkinsonism with rigidity, tremor and inco-ordination.

3. Catatonia. 4. A markedly reduced responsiveness to cutaneous stimuli.

5. Visual stimuli that would elicit responses were a banana in the monkey and a mouse upon which a cat would make an accurately directed pounce,

6. The responses were skimped and of shorter duration than those of the animals before treatment, the forelimbs were rarely used.

7. This oral approach was one of several behaviours, seen to occur spontaneously or in response to an observable stimulus, that also predominates in the infant animals repertoire such as the cat's treading with the forepaws. Symptoms specific to the cat are a violent diarrhoea, inhibited micturation and a loss of appetite. They remain ill for weeks and die in spite of force feeding. No histological change could be found in the brains of these animals, that could not have occurred in the post-mortem delay before fixation. There was no obvious cause of death.

If reserpine has a target area in the brain the evidence points to the basal ganglia. Lesions and stimuli in these structures result in similar motor symptoms, anatomic changes, catatonia and an unresponsive but awake state. Under reserpine, behaviours that reduce the drives of hunger, thirst and sex are abolished, but short-lived "infantile" and predatory actions remain and may reflect a function of the basal ganglia to organize innate behaviours.

SOME BEHAVIOURAL AND PHYSIOLOGICAL EFFECTS OF RESERPINE AND THE CHRONIC ADMINISTRATION OF AMINE-OXIDOSE INHIBITORS IN TRAINED RATS. By J. COLE & D. P. DEARNALEY (*Oxford*).

Fifty-four male albino rats weighting 60-80 g. were divided into thirteen groups of four and one of two.

All animals were trained to a modification of Winter's rope climbing test and their global behaviour observed throughout the experiment, which was designed to study the effects of the chronic administration of the amine-oxidase inhibitors iproniazid, isoniazid, Niamid and T.M.6.

In addition the effects of giving a single dose of reserpine alone to a group of two rats and in combination with iproniazid to three groups of four were recorded.

Three groups of four rats were used as controls; one of these as an additional control received injections of normal saline daily.

Dosage was 100 mg/kg. bodyweight, volume 0·5 ml., injected subcutaneously each day except Sundays for four weeks in the case of iproniazid, isoniazid, or Niamid. T.M.6 was given in a similar manner in doses of 200 mg/kg. bodyweight, but this experiment was stopped by the development of sores at the site of injection.

Reserpine was used in single doses of 5 mg/kg. volume 0·5 ml. Both iproniazid and Niamid produced very considerable impairment of rope climbing performance and gross changes in global behaviour; these decreased almost to vanishing point and rope-climbing recovered during four weeks of daily administration of the drug. Isoniazid which does not inhibit amine-oxidase in vivo did not show these effects.

Reserpine given alone produced the characteristic and well known syndrome, but when administered after two doses of iproniazid this was markedly altered and when given after three weeks of continuous iproniazid almost abolished.

Various physiological phenomena observed after the administration of reserpine are noted and compared with those seen after the amine-oxidase inhibitors.

Concurrent studies of the constituents of the animals' urine were made in an attempt to relate any changes in aromatic, particularly amine, metabolism to their behaviour. This work will be reported elsewhere.

THE EFFECTS OF VARIOUS PHARMACOLOGICAL AGENTS ON THE 'TIMING' BEHAVIOUR OF THE RHESUS MONKEY. By J. M. OXBURY (*London*)

Using a Skinner box (automatic programming and recording) rhesus monkeys were trained on two reward schedules in a bar pressing situation. These schedules were:—

1. Fixed Ratio (FR.15)—animal rewarded following every 15th response;

2. Timing (DRL.20)—animal rewarded if the response was made 20 or more seconds after the previous reward or response.

Daily testing sessions lasted for 80 minutes and were made up of four consecutive 20-minute periods, each period consisting of 5 minutes on FR followed by 15 minutes on DRL. Visual cues indicated which reward schedule was in operation at any particular time.

The measures of performance were:—
On FR—rate of responding (responses/minute).
On DRL—1. *Median* inter-response interval (in seconds);

2. *Spread*—the number of seconds over which the middle 30 per cent. of the inter-response intervals was distributed.

The animals were trained until their performance was stable, and then testing with drugs was begun. Of the changes produced by the various drugs the following were significant at the 0·01 level of confidence in each monkey as compared with control sessions; (3 monkeys were tested with each drug).

Nitrous oxide—increase in the DRL spread.

Ritalin (1·5-3·0 mg/kg. body wt.) decrease in DRL median; decrease in FR response rate.

Reserpine (0·10-0·15 mg/kg.) increase in DRL median.

Meprobomate (150 mg/kg.) no change significant at the 0·01 level of confidence; successive injections produced decreasing changes in all three measures. The DRL median was changed (increase) to a greater extent than the other two measures. Evidence was found of an habituation to meprobomate.

SOME EFFECTS OF MANIPULATING THYROID OUTPUT ON OPEN-FIELD TEST BEHAVIOUR IN THE RAT. By P. L. BROADHURST (*London*)

The subjects for the present experiments were rats from the Maudsley Reactive and Non-reactive Strains (1). These strains have been developed over the past six years by selection for high and low defecation scores in a revised and standardized version of Hall's open-field test (2). In addition to the numerous ways in which the two strains differ behaviourally, it has been shown that physiological, especially endocrine, differences exist (3).

In collaboration with Dr. G. Feuer and with the financial assistance of the Ford Foundation, the thyroid differences were confirmed and attempts made to manipulate thyroid output using thyroid stimulants and depressants. The intention was to observe the effect of such changes on behavioural measures obtained from the open-field test, that is, the defaecation score for which the strains had already been selected, and the ambulation score which measures the exploratory activity of the rat. The design of the experiments involved re-testing treated as well as suitable placebo groups of both strains andsexes in the open field, so that changes in the two scores could be adequately evaluated statistically. To decrease thyroid output propylthiouracil (PTU) was added to the animals' water supply for a month; to increase it two methods were used; injections of thyroid stimulating hormone (TSH) and the addition of potassium iodide to the water. Autopsies demonstrated the efficacy of these treatments, but significant behavioural effects were confined to the group given PTU which showed an increase in defaecation scores with some decrease in ambulation scores. The results were discussed, especially with reference to the strain differences.

REFERENCES

(1) Broadhurst, P. L. (1960). Experiments in psychogenetics: Applications of biometrical genetics to the inheritance of behaviour, in H. J. Eysenck (ed.) *Experiments in Personality*. Vol. I. *Psychogenetics and psychopharmacology*. London: Routledge & Kegan Paul, 1-102.

(2) Hall, C. S. (1934). Emotional behavior in the rat: I. Defecation and urination as measures of individual differences in emotionality. *J. comp. Psychol.*, **18**, 385-403.

(3) Watson, R. H. J. (1960). Constitutional differences between two strains of rats with different behavioral characteristics. *Adv. psychosom. Med.*, **1**, 160-165.

Friday, 16th December

THE ACQUISITION OF NEW BEHAVIOUR PATTERNS

AN ANALYSIS OF SOCIAL FEEDING IN SPARROWS AND CHAFFINCHES. By E. R. A. TURNER (*Cambridge*)

The term 'Social Feeding' is used to describe the situation where the activities of one animal provide the stimuli that elicit feeding behaviour in another animal. Some of the contributory factors leading to social feeding include social facilitation, local enhancement and imitation. In sparrows and chaffinches a feeding bird is more attractive than a non-feeding bird. Social facilitation and local enhancement operate independently but it is suggested that the latter is a

directional component of the former. Neither of these two factors, alone or in combination, will readily lead to social feeding unless the food is familiar. For unfamiliar food, social feeding will much more readily result if the "actor" is consuming similar food, and it is concluded that there is an element of imitation in social feeding. In addition observers feed more readily from unfamiliar microhabitats if other birds are seen feeding from similar situations.

Social feeding is well developed in juveniles, and includes a very strong element of local enhancement. Their imitative ability is less obvious, but is possibly masked by their strong tendency to sample unfamiliar foods and to feed from new microhabitats.

Reciprocal interspecific social feeding occurs between chaffinches and sparrows, but is apparently less strong than the intra-specific behaviour.

THE NATURE AND SPREAD OF *Daphne*-EATING IN THE GREENFINCH, AND THE SPREAD OF SOME OTHER HABITS. By M. PETTERSSON (*London*)

Daphne mezereum L. is a small, fragrant, pink-flowered, pre-vernal shrub. Nowadays the Greenfinch (*Chloris chloris* L.) often eats its seeds, stripping every fruit from the bush. The habit seems to have originated between one and two centuries ago, and to have spread outwards, by cultural diffusion, in a fairly orderly manner (*Nature*, **184,** 649, 1959). The mean date of the seed feast is June 14th, with a standard deviation of $\pm 16\frac{1}{2}$ days.

An extensive co-operative survey has been made of the nature and incidence of this new habit, of this new 'cultural element' of Greenfinch familial societies. The evidence tends to suggest that this cultural element may have been initiated once only. Among Tits *Parus*, this was obviously not the case with bottle-opening.) In Britain, *Daphne*-eating has spread, northwards and southwards, at an overall rate of between 2 and 4 kilometres per year. It has also now reached Ireland and Denmark; but the reports from other continental countries are still negative.

Estimates of the 'overall geographical rate of spread', over several hundred km., of various new cultural elements in other birds and mammals, would be of interest. Such studies could help us to comprehend our own pre-history. For in *H. sapiens*, neolithic agriculture reached Britain from its centre of origin at between $\frac{1}{4}$ and 1 km. per year; bronze-working at about 2 km. per year; and iron-working at something like 5 km. per year (*Biology and Human Affairs*, **25,** 24, 1960; *Nature*, **186,** 870, 1960). And a conceptual model suggests that the new cultural element of 'making stone tools' may well have spread through the australopithecine species first concerned at, again, something like 5 km. per year.

THE ONTOGENY OF SOME LOCOMOTORY AND LEARNING PATTERNS IN TWO SUBSPECIES OF DEER-MICE, *Peromyscus maniculatus*. By J. A. KING (*Bar Harbour*)

Integration of the processes of maturation and learning in the developing animal may partially be determined by the developmental sequence of various sensory-motor modalities. The relative stage of development of different response patterns may goven an animal's experiences and, consequently, the types of things it learns. Early emerging and rapidly maturing behaviour may be reinforced and channelled by the environment to the extent that later emerging behaviour patterns are reduced or eliminated. Heterogenic development of some locomotor and learning patterns in two subspecies of deermice were examined in respect to the differential effect the environment may have upon subsequent development.

Subspecific differences in locomotion and clinging were observed early in development when mice were placed upon an elevated Y maze. These differences were further examined in a swimming test and in an activity wheel. The locomotor responses of *P.m. bairdii* develop earlier than those of *gracilis*, while both subspecies develop clinging responses at about the same age. The differential rates of development of these two responses may contribute to the adult behaviour of both subspecies.

Both subspecies were also tested in an escape learning situation, in which the mice crossed an electrified grid to an insulated platform. The performance of *P.m. bairdii* was marked by an increase in the time spent on the platform from 14 to 20 days of age, whereas *gracilis* showed little change in its performance throughout the testing period. This early development of escape learning demonstrates that each subspecies learns a different type of response to similar environmental conditions, although the subspecific differences cannot yet be ascribed to heterogonic development.

A REVIEW OF RECENT WORK ON THE ACQUISITION OF NEW BEHAVIOUR PATTERNS. By W. H. THORPE (*Cambridge*)

A number of recent lines of experimental study of the development of new behaviour patterns in birds led to the conclusion that there are four aspects of development which emerge as of particular importance. Firstly, there is the question of responsiveness; in birds such as the hand-reared Great Tit this appears to increase with age and then decreases. There are also changes in a different type of responsiveness, namely internal inhibition. Here again there appears to be a rise and also probably a slight subsequent fall with age; but the rates of the first and second changes may be quite different, so the variation in these two factors could well give rise to all the puzzling differences in individual learning ability which experiments such as those of Vince and others on the string-pulling response of passerines have revealed. Thirdly there is the question of the hunger drive and the problem of maintaining approximately the same measure of food deprivation in all the individuals used for experiments. Fourthly, the effects of early experience or environment on behaviour are clearly shown and it seems that internal inhibition may develop more rapidly and more completely in a more varied environment, presumably as a result of greater activity, greater stimulation, and perhaps greater opportunity for adaptation, etc. In this connection, it is plausibly assumed that aviary rearing provides a richer experience for the young bird than does hand-rearing and that rearing in the wild constitutes a richer experience still.

THE STIMULI ELICITING BEGGING IN GULLS AND TERNS. By U. WEIDMANN (*London*)

Work on the sign-stimuli eliciting the begging response of newly hatched Black-headed gulls continues along various lines (cf. previous communication, *Anim. Behav.*, **6**, p. 114). To isolate the effective factors in the total stimulus situation, its different aspects are systematically varied and the effect on the number of pecks given by the chick in 30 seconds is recorded. A black-billed model is superior to a white billed one under "normal" conditions (bright background), but in front of a dark background this is not true (white not quite significantly better than black). The original result is thus at least partly due to brightness differences between bill and background. The inter-action between different factors (heterogeneous summation) was studied quantitatively.

The perceptual abilities of gulls were assessed in three ways: (1) the maximum extent of the field of vision of the chicks was determined morphologically and it was concluded that they could not see the head region of our models while pecking at the bills; this explains some previous results, e.g. the negligible influence of head colour on pecking score. Indeed, smaller models of a slightly different design (as a chick would see the adult from underneath) showed that head colour may influence the response mainly by its contrast with bill colour. The earlier conclusion that the brown mask of the parent is not an adaptation to the feeding situation was confirmed.

(2) Physiological evidence concerning the coloured oildroplets in the cones of the bird retina suggested to us a theory for the unexpected result that Ostwald blue 13 elicited nearly as many pecks as the reds, unlike blue 16, which was much worse. From the reflection curves of the papers in question and the absorption characteristics of red and yellow oil droplets we suggested that blue 13, but not blue 16, was seen as a sort of dark red.

(3) This theory was tested as follows. The begging response can be conditioned to a model, by rewarding each peck with food; after 50 rewarded pecks even a grey disc, otherwise a bad model, elicits more pecks than the hitherto best model, a red rod. Positive conditioning to blue 13 is generalised to blue 16 but not to red 7 or mixtures of red 7 with black. This suggests that for these chicks, as for man, blue 13 looks more like blue 16 than red.

Figures with a well defined centre, which may facilitate aiming, elicit more pecks than do models which on other grounds might have been considered to be superior. We conclude that a stimulus situation may elicit more pecking than another for various reasons; e.g. it may be more easily noticed or it may be more successful in holding the attention. While we cannot yet assess the precise contributions of general preception and specific filtering effects of the IRM to the chick's responsiveness to various stimulus situations, the experiments strongly underline

the selective advantage which "conspicuousness" confers on a releaser.

Comparing different species of terns and gulls it appears that many young react better to red models than to others; the adult bill (or at least part of the bill) in these species is red. That this coincidence is not due to chance is suggested by experiments in 2 species with black bills; in the Sandwich tern I found that the young prefer black to red, and in the Wideawake tern (experiments of J. M. Cullen) there is no preference either way. In the absence of data on the preference of young of other waders (the majority of which do not feed their young) it is impossible to say whether the well-nigh ubiquitous occurrence of red on the bill of Laridae is an adaptation to the innate preference of the young in the first place, or vice versa.

EXPERIMENTS ON HOST FINDING BY THE TSETSE FLY, *Glossina medicorum*. By R. F. CHAPMAN (*London*)

Laboratory experiments on *Glossina medicorum* showed that it was stimulated to become active by a moving object and that it responded by moving towards the object and landing on it. *G. medicorum* did not respond to objects more than 25 ft. away in the field but *G. morsitans* responded up to 150 ft. *G. medicorum* was also activated by the smell of cows and orientated upwind in a wind-tunnel. It was concluded that in all probability both vision and smell, aided by orientation to air movements, were important in host-finding, vision being more important when close to the host.

FACTORS AFFECTING THE DEVELOPMENT OF THE SMILING RESPONSE AS A SOCIAL RELEASER IN HUMAN INFANCY. By J. A. AMBROSE (*London*)

The hypothesis is advanced that smiling in human infancy becomes an automonous greeting response derived from low-intensity laughing. Although the smiling motor pattern is the same in each, the responses of smiling and of laughing are regarded as distinct responses since they differ in developmental characteristics, intensity-range, causation and function. Smiling as a greeting response develops to full intensity much earlier than the laughing response and even later does not go over into laughing. The eliciting stimuli, although at first unspecific, became increasingly limited: first any human eyes, then the configuration of any whole face, then individual familiar faces only. The characteristic effect of the response, through increasing the infant's attractiveness, is to increase the mother's readiness to respond to her infant. The mother's change in mood may be manifested in a general way by her increasing or maintaining the quality of her caring activities, but it is often expressed in a specific way by her smiling back and talking to her infant and perhaps also picking him up, holding, and caressing him. This type of response by the mother results in a drop in the motivation of the infant's smiling and reinforces the response. Infants reared with only the bare minimum of physical care and without such "social stimulation" show retarded motor, intellectual and emotional development and a relatively high mortality rate. It is suggested that the infant's smiling response, a simple, conspicuous and distinctive one, is a social releaser the function of which is to increase the infant's chances of survival and healthy development through increasing the stimulation received from the mother beyond that which ordinarily accompanies physical care. Since the human infant in this period is unable to achieve such stimulation unaided, by following or clinging to his mother, it is necessary that he be equipped with means of attracting her to him to this end.

THE DEVELOPMENT OF FEEDING BEHAVIOUR IN BABIES' FIRST DAYS OF LIFE. By MAVIS GUNTHER (*London*)

Western European mothers do not always know how to feed their first babies from the breast. The suggestion is made that in man this failure might be attributable to lack of opportunity for mimicry.

The mother's part in getting a baby to feed from the breast is to provide transport and to put the baby in position. The baby's feeding behaviour is not brought into action by this alone but is dependent on the baby experiencing a time when he draws the nipple or its substitute to the back of his mouth. Where the nipple and areola are easily protractile eager feeding may be established immediately. Where the protractil-

ity is only moderate the successful arousing of eager feeding may not be achieved until better positioning enables the baby to get a longer hold and may be observed to start from that one occasion. Where this is not achieved and no nipple substitute is given, the baby may remain an apathetic feeder. The consistency of the response in which babies change from apathetic feeders to active seekers of the breast and active feeders, the apparent purposive co-ordinated activity and the change in behaviour without previous experience, indicate that feeding in the neonate is an instinctive behaviour. It is evoked by the pattern of stimuli provided by the nipple and areola tissues in the mouth. A bottle teat can also act as a releaser and can be super-normal to poorly formed breasts. The baby's mouth response may then rapidly become altered and suited only to receiving the thrust of the bottle teat.

Feeding behaviour of a baby in the first days of life shows these three patterns, immediate active feeding, apathy until feeding is aroused, and lasting apathy, and a fourth—fighting at the breast. This arises where the baby has had his nostrils covered, usually by his upper lip, when put to the breast. When brought to the breast the baby cries, arches his back away and boxes with his hands. This appears to be conditioned response.

A film showing these types of behaviour was shown.

PROCEEDINGS OF THE SECTION OF ANIMAL BEHAVIOR AND SOCIOBIOLOGY (ECOLOGICAL SOCIETY OF AMERICA AND THE AMERICAN SOCIETY OF ZOOLOGISTS)

The following papers were read in New York in conjunction with the annual meeting of the American Association for the Advancement of Science. The symposium on Teaching Animal Behaviour was co-sponsored with the National Association of Biology Teachers and Section F of the AAAS.

Abstracts of the papers are available in the *Anatomical Record*, **138(3)**, 1960.

Wednesday Morning, December 28th, 1960

ANIMAL BEHAVIOR AND SOCIOBIOLOGY, I. EARLY EXPERIENCE

HELEN BLAUVELT presiding

EARLY PREDATORY BEHAVIOR IN PRAYING MANTIDS. By SOL KRAMER, *State University of New York*

THE IMPRINTING OBJECT AS A REINFORCING STIMULUS. By B. A. CAMPBELL and J. R. PICKLEMAN *Princetown University*.

DEVELOPMENTAL AGE AS A BASELINE FOR DETERMINING THE CRITICAL PERIOD IN IMPRINTING. By GILBERT GOTTLIEB, *Duke University*.

INFANTILE EXPERIENCE WITH SPECIFIC VISUAL STIMULI AS RELATED TO LATER DIFFERENTIAL APPROACH RESPONSES IN RATS. By ETHEL TOBACH, L. VROMAN, G. TURKEWITZ & T. C. SCHNEIRLA, *American Museum of Natural History*.

EFFECTS OF EARLY SOCIAL EXPERIENCE ON AGGRESSIVE PLAY IN YOUNG GOATS. By HELEN BLAUVELT & A. ULRICH MOORE, *Upstate Medical Center in Syracuse and Cornell University*.

ANIMAL HYPNOSIS (TONIC IMMOBILITY) CONSIDERED AS A PARAMETER OF BEHAVIOR IN DISTINGUISHING BETWEEN A GROUP OF NORMAL AND ABNORMAL (EXPERIMENTAL) LAMBS AND KIDS. By A. ULRIC MOORE & MARVIN AMSTEY, *Cornell University*.

EFFECTS OF GRADED AND DELAYED EXPERIENCE ON BEHAVIORAL DEVELOPMENT IN PUPPIES. By JOHN L. FULLER, *Jackson Memorial Laboratory*.

RESPONSE TO NESTING MATERIALS BY WILD-BORN AND CAPTIVE-BORN CHIMPANZEES. By IRWIN S. BERNSTEIN, *Laboratories of Primate Biology, Orange Park, Florida*.

Wednesday Afternoon, December 28th

ANIMAL BEHAVIOR AND SOCIOBIOLOGY, II

C. R. CARPENTER presiding

PERSISTENCE OF A CONDITIONED RESPONSE IN THE CICHLID FISH, *Tilapia macrocephala*, AFTER FOREBRAIN AND CEREBELLAR ABLATIONS. By LESTER D. ARONSON & RONALD HERBERMAN, *American Museum of Natural History*.

PHYSIOLOGICAL EFFECT OF PREWEANING MANIPULATION IN TWO STRAINS OF RATS. By LEO VROMAN, E. TOBACH, G. TURKEWITZ & T. C. SCHNEIRLA, *American Museum of Natural History*.

AGGRESSIVE BEHAVIOR IN THE SOCIAL ORGANIZATION OF GOATS AND SHEEP. By HELEN BLAUVELT & A. ULRIC MOORE, *State University of New York and Cornell University*.

FLIGHT AND SWIMMING REFLEXES IN GIANT WATER BUGS. By HUGH DINGLE, *University of Michigan*.

ECOLOGICAL SIMILARITY AND CANNIBALISTIC INTERACTION IN THE MONARCH AND QUEEN BUTTERFLIES, *Danaus plexippus* and *D. berenice*. By LINCOLN P. BROWER, *Amherst College*.

A STUDY OF HOMING IN THE COTTON MOUSE, *Peromycus gossypinus*. By JAMES V. GRIFFO, Jr., *Fairleigh Dickinson University*.

POPULATION ANALYSIS, GROUP COMPOSITION AND BEHAVIOR OF HOWLER MONKEYS *(Alouatta palliata)* OF BARRO COLORADO ISLAND IN 1959. By C. R. CARPENTER, *Pennsylvania State University*.

CONSUMER BEHAVIOUR: INNER-ORIENTATION OF POPULATION IN A FUNCTIONAL AREA. By ERNEST M. KUHINKA, *Dickinson College*.

Thursday Morning, December 29th, 1960

ANIMAL BEHAVIOR AND SOCIOBIOLOGY, III. SEXUAL BEHAVIOUR

EVELYN SHAW presiding.

A QUANTITATIVE STUDY OF THE COURTSHIP BEHAVIOR IN THE QUEEN BUTTERFLY, *Danaus berenice* (Cramer). By LINCOLN P. BROWER & FLORENCE P. CRANSTON, *Amherst College and Harvard Medical School*.

SEX DISCRIMINATION IN SPECIES OF *Colisa* and *Trichogaster*. By ANTHONY R. PICCIOLO, *University of Maryland*.

COLOR CHANGES CORRELATED WITH PARENTAL BEHAVIOR IN CICHLID FISH. By SOL KRAMER, *State University of New York*.

SPAWNING AND PARENTAL BEHAVIOR IN FEMALE PAIRS OF THE JEWEL FISH, *Hemichromis bimaculatus* Gill. By BERNARD GREENBERG, *Roosevelt University*.

EFFECT OF TESTOSTERONE ON OCCURRENCE OF SOME DUCK DISPLAYS. By RICHARD E. PHILLIPS & D. FRANK McKINNEY, *Cornell University and Delta Waterfowl Research Station*.

A MOTIVATIONAL INTERPRETATION OF THE GREETING DISPLAY IN GEESE. By ROBERT B. KLOPMAN, *Cornell University*.

ROLE OF HEAD HEIGHT IN RELEASING SEXUAL VERSUS FIGHTING BEHAVIOR IN TURKEYS. By E. B. HALE, *Pennsylvania State University*.

SOME ASPECTS OF BEHAVIORAL EVOLUTION. By ROBERT W. FICKEN, *Cornell University*.

THE EVOLUTION OF AGONISTIC, PRE-COPULATORY AND NEST-BUILDING BEHAVIOR IN THE AFRICAN PARROT GENUS *Agapornis*. By WILLIAM C. DILGER, *Cornell University*.

Thursday Afternoon, December 29th

ANIMAL BEHAVIOR AND SOCIOBIOLOGY, IV. SEXUAL BEHAVIOUR AND COMMUNICATION

J. L. FULLER presiding

SEXUAL BEHAVIOR IN INBRED STRAINS OF MICE. By THOMAS E. McGILL, *Williams College*.

CHANGES IN SEXUAL BEHAVIOR IN SPAYED FEMALE GUINEA PIGS FOLLOWING HYPOTHALAMIC LESIONS. By LARRY L. MORGENSTERN, *University of Kansas*.

ACOUSTICAL BEHAVIOR AND COURTSHIP OF CONENOSE BUGS *(Himiptera, Reduviidae, Triatominae)*. By THOMAS E. MOORE, *University of Michigan*.

AN EXPERIMENTAL ANALYSIS OF THE SINGING BEHAVIOR OF THE TRUE KATYDID *(Pterophylla:* Tettigoniicae). By KENNETH C. SHAW, *University of Michigan*.

THE SIGNIFICANCE OF SOUND PRODUCTION DURING THE REPRODUCTIVE BEHAVIOR OF *Notropis analostanus*. By JOHN F. STOUT, *University of Maryland*.

SOUND PRODUCTION OF SQUIRREL FISHES. By HOWARD E. WINN & JOSEPH MARSHALL, *University of Maryland*.

SOUND SPECTOGRAPHIC ANALYSIS OF A CONTINUOUS SINGER, THE MOCKING BIRD. By D. K. HUNTER & ROBERT SELANDER, *University of Texas and American Museum of Natural History.*

THE ROLE OF LEARNING IN THE DEVELOPMENT OF THE EASTERN BLUEBIRD'S VOCAL REPERTOIRE. By JAMES M. HARTSHORNE, *Cornell University.*

Friday Morning, December 30th, 1960

Symposium: TEACHING ANIMAL BEHAVIOUR, 1. ANIMAL BEHAVIOUR IN BIOLOGY TEACHING

E. B. HALE presiding

INTRODUCTION TO THE SYMPOSIUM. E. B. HALE, *Pennsylvania State University.*

ANIMAL BEHAVIOR AS A BIOLOGICAL DISCIPLINE. By J. P. SCOTT, *Jackson Memorial Laboratory, Bar Harbor, Maine.*

ANIMAL BEHAVIOR IN COLLEGE BIOLOGY. By B. E. GINSBURG, *University of Chicago.*

ANIMAL BEHAVIOR IN SECONDARY-SCHOOL BIOLOGY. By A. J. BAKER, *Crystal Lake High School, Crystal Lake, Illinois.*

Friday Afternoon, December 30th

Symposium: TEACHING ANIMAL BEHAVIOR, II. TECHNIQUES IN TEACHING ANIMAL BEHAVIOR

ARTHUR J. BAKER presiding

FILM INSTRUCTION. By C. R. CARPENTER, *Pennsylvania State University.*

VERTEBRATE MATERIALS. By W. C. DILGER, *Cornell University.*

INVERTEBRATE MATERIALS. By THOMAS SMYTH, Jr., *Pennsylvania State University.*

SPECIAL PROJECTS. By WALTER GOHMAN, *Iowa State Teachers College Laboratory School,*

OPEN DISCUSSION.

BOOK REVIEWS

Antibiotics: Their Chemistry and Non-Medical Uses. Edited by H. S. GOLDBERG, with contributions by P. REGNA, C. L. WRENSHALL, T. D. LUCKEY, R. N. GOODMAN and J. D. LOGUE, and a foreword by PAUL R. BURKHOLDER. Princeton, N.J.: D. Van Nostrand, 1959. Pp. 618. 112s. 6d.

The seven chapters in this timely work deal respectively with historical and other introductory aspects, the chemistry of antibiotics, antibiotics in nutrition, the influence of antibiotics on plants and plant disease control, antibiotics in food preservation, antibiotics in the isolation and cultivation of micro-organisms, and the public health significance of the whole subject.

Those workers concerned with animal behaviour studies will be interested in Dr. Luckey's chapter on antibiotics in nutrition and the suggested explanation of the means whereby such variables as bodyweight gain, intestinal thickness and the gut flora are influenced by feeding these materials, and "stress factors" are combatted.

Luckey adopts the view, perhaps wisely, that the mode of action of dietary antibiotics in "growth stimulation" is complex, and devotes several pages to an assay on hormoligosis. Many workers must be satisfied, however, that in chicks at least the clear-cut findings of the Shinfield workers, coupled with the inability of antibiotics to influence the gain of "germ-free" individuals, provide a rational explanation of the majority of recorded effects. Luckey, however, accepts results indicating that very small amounts of antibiotic stimulate the growth of germ-free chicks, and considers that they are in accord with the Arndt-Schultz rule. It is clearly of great importance to establish whether antibiotic supplements act on host tissues as such or entirely through modification of intestinal or other micro-organisms, but the evidence to date surely supports the view that low-grade infections are the major factor in the "stress" conditions that antibiotics are used to combat.

The documentation of the book as a whole, and of Luckey's chapter in particular, is excellent and the work forms a valuable resume of a field that has grown enormously from its inception little more than a decade ago.

A.N.W.

British Medical Bulletin. Vol. 16. No. 1. *Antibiotics in Medicine.* The British Council. 20s.

The magic wand of the antibiotics has waved over medicine for nearly two decades, with remarkable benefits but with much evidences of misuse. The outcome of the latter is becoming ever more apparent in the "resistant strains" or "hospital infections" that are known to inhabit both premises and staff in contact with these substances for any length of time.

Detailed studies ranging from the synthesis, detailed structure, mode of action and toxicity of the substance concerned, to the laboratory control of treatment are discussed in this recent and timely addition to the series. Each issue of the *British Medical Bulletin* is a textbook in itself, and all who are concerned in any way with the medical and allied uses of antibiotics will find this particular publication of real value.

A.E.S.

Pet Chihuahua. By TERESA E. THURMER. Fond du Lac, Wis.: All Pets Books Inc. Illustrated. (1959). $1.00.

This has been selected as one of a considerable series dealing with individual breeds. It is well illustrated and attractively produced, and contains much practical information of value. There has undoubtedly been a considerable advance in the value of the information provided in works of this kind during recent years, with consequent benefit to the dog owner.

A.N.W.

The Cult of the Budgerigar. By W. WATMOUGH. London: Cage Birds. 5th ed. 1960. Pp. 256. 30s.

The latest edition of this well-known work follows the same pattern as its predecessors and is, of course, a mine of information to the budgerigar fancier, although unfortunately not documented sufficiently for other purposes. The illustrations are excellent and the author has clearly worked hard to maintain the indispensible nature of his work. It is written primarily for those who breed budgerigars for exhibition purposes, and the information is essentially practical.

The chapter on food and feeding, while useful, does not take all recent information—scanty though this is—into account.

A.N.W.

Grass Productivity. By A. VOISIN (Translated by CATHERINE HERRIOT). London: Crosby Lockwood. 1959. Pp. 368. 50s.

The back of the dust cover of this work, and also the reverse side of the last page of the index, are devoted to a forthcoming book by the author entitled *Soil, Grass and Cancer* and affirms that M. Voisin is ". . . . neither a crank nor a lone voice." It is difficult, although quite unfair in the absence of further information, to dismiss such a lurid title from one's mind while reading the present text. Fortunately, however, the work now reviewed appears to be free from fanciful hypotheses. On the contrary, it is better documented than the majority of French agricultural texts and indicates a wide survey of British, German, and, to a somewhat lesser extent, American publications, and some of the grazing behaviour studies reported to the Association for the Study of Animal Behaviour are given due consideration.

The twelve principal sections in which the text is divided deal, respectively, with the grass; the cow; laws of rotational grazing; principles for the conduct of rational grazing (the term employed by the author to intensive grazing); rational grazing in practice; common errors; tethering and other special systems; division of pastures; effect of rational grazing on the flora; and three final discussions summarizing present knowledge and considering the future. The whole forms a useful and readable work for anyone interested in this vast and economically important subject, and is well-produced.

A.N.W.

Research in Veterinary Science: A Journal of the British Veterinary Association. Vol. 1, No. 1., January, 1960. Oxford: Blackwell. Pp. 104. Published in January, April, July and October of each year, annual subscription 90s.

Until comparatively recently the principal U.K. journals devoted to Veterinary Science comprised the weekly *Veterinary Record*, the monthly *British Veterinary Journal* and the quarterly *Journal of Comparative Pathology and Therapeutics*. Many papers of a veterinary nature were, of course, published in specialist journals but it appears to be the opinion of many in the field that further journals are required, hence the appearance of the present publication—devoted to original contributions to knowledge on the health and disease of animals—and, almost simultaneously, of the *Journal of Small Animal Practice*.

This first issue comprises, as might be expected, papers of a type that hitherto were interspersed with non-research and clinical contributions in the *Veterinary Record*. It is the stated policy of the weekly B.V.A. publication to continue to publish original scientific papers, but that there may be an adequate additional supply for their new quarterly is indicated by the contents of this first issue. One manuscript has been with the editors since February, 1959, but the remainder were all received between late July and late October. Whether such promptness in publication may be maintained as the journal becomes established remains to be seen. Contributions, in English, are invited from any quarter.

The papers in this first issue, to which the President of the B.V.A. contributes a foreword—include those related to *Escherichia coli* (two) and enteroviruses (three) associated with the pig; gastro-intestinal nematodes of cattle; the growth and isolation of *Brucella*; facial eczema of sheep; canine distemper/hepatitis vaccine; tumours of the central nervous system of dogs; and the relationship between toxicity and coccidiostatic efficacy for chicks of pyrimethamine and sulphonamides, and their reversal by folic acid.

The journal is well and clearly produced and the quality of the paper permits of good reproduction of text figures and photographs. There is an impressive editorial board, and it is to be hoped that this new venture will accelerate the publication of papers of good quality.

A.N.W.

Blood Groups. British Medical Bulletin, Vol. 15, No. 2. London: British Council. 20s.

The study of Blood Groups has been the focus of attention of a vast number of highly specialised research workers. It has therefore been almost impossible to keep up to date with all the ramifications of the subject that are so surely being unravelled. There can be few who are concerned with medical or biological research who will be unable to find something bearing on their own particular problems in this symposium of 15 contributions by distinguished workers in this field.

Of particular comparative interest "The Relation Between Animal and Human Blood Groups" by Valerie C. Joysey. To quote: "It has been observed that individuals heterozygous at several blood-group loci are superior to

homozygotes in reproductive ability and viability." How often has this factor been taken into account in assessing experimental results?

A.E.S.

Development of the Poultry Industry in England and Wales 1945-1959. By R. COLES. London: Poultry World. 1960. Pp. 80. 7s. 6d.

The author, who is Chief Poultry Advisory Officer to the Ministry of Agriculture, Fisheries and Food, has access to all relevant statistical information, but is nevertheless to be congratulated on the succint and readable way in which he has handled them. This work deserves the closest study by all who are concerned with the economics of the poultry industry—and by all others interested.

The changing patterns of the industry are clearly set out and, where possible, analysed. Thus ". . . what is still the major weakness of the British broiler industry, namely, the quality of the bird" is amply discussed and set out in contrast to the overall improvement in performance that has come from other developments—and which in consequence has proved expensive.

A.N.W.

Poultry Nutrition. Bulletin of the Ministry of Agriculture, Fisheries & Food. By W. BOLTON. London: H.M. Stationery Office (dated May, 1959, published February, 1960). Pp. 96. 5s.

The well-known Bulletin No. 7 in this series, *Scientific Principles of Poultry Feeding*, was last issued in 1950, and there was clearly need for extensive revision or a completely new work. The latter course has been chosen and Dr. Bolton who has been a leading worker in this field since the last war, has been entrusted with the task. It is presumably indicative of one of the many unfortunate consequences of the printing strike of 1959 that the actual date of publication was some nine months after that appearing on the flyleaf.

The author is to be congratulated on his thoroughness and on the readable information that he has condensed into fewer than 100 pp. of text, and also on his attempt to adhere to the correct usage of the terms "ration", "diet", "mash", "food" and "feed". In view of his own studies, it is not surprising that he should make firm recommendations concerning the evaluation of dietary energy and in particular that determinations of "available carbohydrate" should be substituted for those of crude fibre in conventional analysis.

It is understandable that in an official publication some modern developments should receive scant attention and the whole subject of unidentified factors is discussed in half-a-page as being principally of scientific interest. This, togehter with the remarks on p. 34 concerning the standardization of dried distillers' solubles, may call for some comment from industry, particularly since a type of solubles is incorporated in one of the rations in use at the National Institute of Poultry Husbandry, and cited in the appendix tables. These tables provide much useful information and might have been extended in certain cases so as to simplify calculations on the ration itself as well as on the bird's needs.

A.N.W.

Machine Milking. Bulletin No. 177 of the Ministry of Agriculture, Fisheries & Food. London: H.M.S.O. 1959. Illustrated. 12s. 6d.

This entirely new work has been prepared by the staff of the National Institute for Research in Dairying, under the general supervision of Dr. A. T. R. Mattick, who, until recently, was Director. It provides a much-needed text, for there is no other work in the English language that deals with the subject in sufficient detail.

The work is divided into six sections dealing respectively with the anatomy and physiology of the udder, engineering aspects, use of the milking machine, milking machines and mastitis, hygiene and rubber. Each section is adequately referenced, and the last goes back to first principles and discusses the molecular make-up of rubber, manufacture, properties and ageing, and the important question of deterioration of liners.

The section dealing with milk ejection has been written with full reference to current information, available in the fields of physiology and behaviour, and all those concerned are to be congratulated on this extremely useful and important work. A.N.W.

Aviaries, Birdrooms and Cages. By L. P. LUKE & ALLEN SILVER. Cage Birds, London, 6th ed. Illustrated. 7s. 6d.

This clearly-written and well-illustrated book deals adequately with its subject, and is full of practical information, some of which the reviewer and his colleagues have already used. It is, of course, clear that the living conditions of captive birds have as yet received little scientific study from the standpoint of hygiene, ventilation and environmental requirements, but this need not detract from the usefulness of the present work. A.N.W.

Comparative Breeding Behavior of Four Species of North American Herons. By ANDREW J. MEYERRIECKS (1960). Pp. viii + 158, with 39 figures and 20 tables in the text and 15 plates. Publication No. 2 of the Nutta Ornithological Club, Cambridge, Mass.

This is the most imporant study of the behaviour of herons since Verwey's paper on the Grey Heron, and it is the first really comparative account. The main part consists of a detailed description of the behaviour of the Green Heron *Butorides virescens*; less complete but still extremely useful descriptions are further given of the Great Blue and the Great White Heron (considered to be conspecific: Ardea *herodias*), The Reddish Egret *Dichromanassa rufescens*, and the Snowy Egret *Leucophoyx thula*. Of each species the distribution and description, the maintenance activities, migration and behaviour on arrival, hostile behaviour, sexual behaviour and early pairing behaviour are dealt with. The work concludes with a chapter on some evolutionary trends in heron behaviour.

The descriptions, greatly aided by excellent sketches and many tables, are admirable and will for a long time be an indispensable basis for future studies. The author himself points out that for a full evolutionary interpretation many more species will have to be studied; a more penetrating analysis of causation, function, likely origin and ritualisation will also be required. Nevertheless his work, accomplished singlehandedly in a few years, is a great step forward. For instance, very convincing evidence is given of the function of several behaviour patterns: some displays are shown to repel trespassers and to attract sex partners; the wings-spread stance during feeding which the Reddish Egret uses almost as much as the African Black Heron ("canopy feeding") is shown to lure fish into this false cover which are then rapidly snapped up. A great deal of evidence is given which supports the idea that displays are due to dual or even multiple motivation (though a more critical treatment of the methods applied would have been welcome). The comparison brings out the basic similarity in the displays of the various species and the interesting interspecific variations of this common theme, such as the greater mobility of the smaller species which allows aerial displays, and the correlation between displays and epigamic structures ("A Snowy Egret in the Forward Display is 'all feathers' "—p. 129). When the evolutionary chapter appears a little meagre, this is probably due to the author holding his fire until his studies of more species will be published.

N.T.

Stress and Psychiatric Disorder. J. M. TANNER, Ed. (1960). Pp. iv + 151. Oxford: Blackwell Scientific Publications. 21s.

This volume records the proceedings of a four-day conference, of 37 members, held by the Mental Health Research Fund at Lincoln College, Oxford, in July, 1958. In view of the commendably few papers it seems surprising, and perhaps indicative of the growing importance of the topics discussed, that some 23 months elapsed before publication. The appearance of the papers and accompanying discussions is nevertheless most welcome, for the subject matter is stimulating and provides strong support for the view that animal behaviour studies are of real comparative as well as intrinsic value: the date of the conference helps to explain the fact that one only of the 74 selected references is to this journal.

The proceedings are divided into six chapters, the first being a readable introduction by Sir Geoffrey Vickers on the concept of stress in relation to the disorganization of human behaviour. The second, called also the disorganization of behaviour in man, contains three papers by Erich Lindemann, H. G. Wolff and E. J. Anthony. Lindemann's paper is based partly on his published work on bereavement. Wolff reviews stressors as a cause of disease, and includes a summary of a large-scale study by Dr. Lawrence Hinkle and his colleagues, working in the Human Ecology Program at the New York Hospital and Cornell University Medical College. This is followed by a report of a lively discussion, including a detailed account of "Some current usages of the word 'stress' in different fields" by Derek Richten. E. J. Anthony discusses the effects of training under stress in children, with conclusions that would appear to be comforting to the parent that is neither lax nor over-fastidious. The third chapter deals with the disorganization of behaviour in animals. In it R. A. Hinde discusses the ethological approach in a most able manner, and it is clear from the general discussion in chapter 6—as well as for the lengthy specific discussion—that his views are helpful to clinicians and others concerned with human problems.

Howard S. Liddell, dealing with experimental neurosis in animals, discusses in some detail a

few observations on sheep and goats for which he and his colleagues have been responsible. It would appear from some of their later studies that the dramatic results obtained need replication in order to put their signifiance beyond doubt. The fourth chapter, a physiological responce to stressors, opens with a paper by Hans Selye on the concept of stress in this context, which is brief in view of his semi-popular work on *The Stress of Life* and his monograph on *The Chemical Prevention of Cardiac Neuroses* that appeared shortly before the conference was held. Hudson Hoagland deals primarily with the investigations of his colleagues and himself at the Worcester Foundation on endocrine stress responses, and adds to the information in the valuable series of publications that have appeared since 1943. In many ways this paper is the most exciting in the book and provides ample evidence of the significance of the findings to date and of the great scope for this field of study. The fifth chapter deals with the prevention and treatment of psychiatric reaction to stress, and opens with a paper by W. Linford Rees who discusses physiological and pharmacological procedures. This topic has, of course, formed the theme, or partial theme, of various other conferences and symposia during the past few years. J. D. Sutherland discusses psychosocial means, and his lucid contribution is followed by a detailed discussion opened by Eric L. Trist, who includes reference to studies in work organization at the coal face, published by G. W. Higgins in *Human Relations* (Vol. 13, No. 1). The final chapter, the general discussion, comprises two contributions by Denis Hill and by Ralph Gerard respectively. Hill pleads that the conference might well direct its attention not so much to the effects of stress but to the stress state itself, the process of reaching a new adaptation. Gerard quotes extensively from his own lecture given shortly before the present conference to the New York Academy of Medicine, in which he attempts "... the transliteration, asked for by several people, from the pscyho-social to the neuro-physiological." One can but hope that this brave attempt is near to successful, for the gap he attempts to bridge is the most serious of the many which faces behavioural science. A definition that he offers elsewhere might cause philosophers to boggle, viz. "Living is essentially a continuous tracking performance at the mental or judgemental level, based on the best probability expectations that the organism can toss up from its experience," but his remarks leading up to it make for highly interesting reading.

Altogether the contributions fully justify the foreword on the Fund by its Chairman, I. T. Henderson, and the modest price of this volume should ensure its wide distribution among the many who will benefit from its perusal.

A.N.W.

BOOKS RECEIVED

The following books have been received and in appropriate cases will be reviewed as space permits in early issues.

John L. Fuller (1960)
Behaviour Genetics
London: John Wiley & Sons 72s)
John L. Fuller and W. Robert Thompson (1960.

A. E. Harrop (1960)
Reproduction in the Dog
Baillière, Tindall & Cox, London: 30s.

Kai Curry-Lindahl (1960)
Ecological Studies on Mammals, Birds, Reptiles and Amphibians in the Eastern Belgian Congo, Part II
Tervuren

M. G. Elwin (1960)
Tropical Fishes
London: Poultry World Ltd. 2s. 6d.

British Poultry Standards (revised edn.)
'Poultry World' London (1960) 35s.

Joint WHO/FAO Expert Committee on Zoonoses. Second Report. Published jointly by FAO and WHO and issued also as *World Health Organization: Technical Report Series*, No. 169

Eric Golden
Broilers Production and Management
London: Poultry World 10s. 6d.

Animal Psychology Seminars
Pergamon Press 25s.

J. A. Deutsch (1961)
The Structural Basis of Behaviour
Cambridge University Press 30s.

Andre Voisin (1960)
Better Grassland Sward, Ecology, Botany and Management
London: Crosby Lockwood & Son, Limited. 42s.

British Medical Bulletin, Volume 17
London: Medical Department, The British Council 20s.

W. H. Thorpe & O. L. Zangwell (eds.) (1961)
Current Problems in Animal Behaviour: A Survey
Cambridge University Press 45s.

R. H. Smythe, M.R.C.V.S. (1958)
The Mind of the Dog
Country Life Limited 18s.

R. H. Smythe, M.R.C.V.S. (1957
What Makes a Good Horse
Country Life Limited 21s.

R. H. Smythe, M.R.C.V.S. (1959)
How Animals Talk
Country Life Limited, London 18s.

R. H. Smythe, M.R.C.V.S. (1960)
The Female of the Species
Country Life Limited, London 21s.

Calf Rearing
Ministry of Agriculture, Fisheries & Food. 3s.

ERRATA

In the paper by Erica Eisner appearing in Vol. VIII, pp. 155-179, the following corrections should be noted.

P. 160, 2nd column, lines 51-53, should read ". . . so that the whole physiological system concerned with prolactin may also be *atypical* in their case."

P. 166, 1st column, second paragraph, should commence "The male domestic pigeon shows constant spermatogenesis and sex drive except when it is incubating or feeding young."

DICTIONARY OF BEEKEEPING TERMS

WITH ALLIED SCIENTIFIC TERMS
edited by Dr. Eva Crane

now available in two volumes

VOLUME I:
ENGLISH — FRENCH — GERMAN — DUTCH

VOLUME II:
ENGLISH — ITALIAN — SPANISH

each volume is available bound in cloth at 16/- ($2.80), or bound in board at 12/6 ($2.25).

The two volumes together make it possible to translate the 1500 terms listed from any one of the six languages represented into the other five. About half the entries are zoological terms.

BEE RESEARCH ASSOCIATION

Hon. **Publications Secretary, 11 Poplar Grove, Maidstone, Kent**

For your books and journals

you cannot do better than to consult our Sales Department. We shall be pleased to welcome you at our Showrooms, just off the Strand, where you may inspect our extensive stocks of the scientific books of all publishers (including books and periodicals mentioned in this Journal). If you are not in London, order your books from us by post: we can supply promptly by mail either individual copies or large institutional orders. We can send books and periodicals to any address in any part of the world. Address all your enquiries to

THE SALES DEPARTMENT
BAILLIERE, TINDALL AND COX LTD.
7 & 8 Henrietta Street, London WC2

VALUABLE RESULTS OF BEHAVIOUR RESEARCH

ZEITSCHRIFT FÜR TIERPSYCHOLOGIE

JOURNAL OF ANIMAL PSYCHOLOGY

EDITED IN COLLABORATION WITH LEADING EXPERTS

by

PROF. DR. O. KOEHLER Freiburg/Br. and **PROF. DR. K. LORENZ** Seewiesen/Obb.

Zeitschrift für Tierpsychologie publishes original works and lectures about the whole field of research of behaviour and animal psychology in German, English, French and Italian. Each essay is followed by a short summary in German and English.

Articles included in vol. 17 (1960), Issues 5 and 6:

LARSSON, K., Effects of enforced intervals on the mating behaviour of Rats of different ages.

DIETERLEN, F., Bemerkungen zu Zucht und Verhalten der Zwergmaus (*Micromys minutus soricinus* Hermann). (Breeding and behaviour of the harvest-mouse).

BOVET, J., Experimentelle Untersuchungen uber das Heimfindevermogen von Mausen (Experimental research on the ability of mice to find their way home).

DILGER, W. C., The Comparative Ethology of the African Parrot Genus Agrapornis.

MOHR, H., Uber die Entwicklung einiger Verhaltensweisen bei hand-aufgezogenen Sperbern (*Accipiter n. nisus* L.) und Baumfalken (*Falco s. subbuteo* L.). (Development of some manners of behaviour in breeding of sparrow-hawks (*Accipiter n. nisus* L.) and falcons (*Falco s. subbuteo* L.).

VERLAG PAUL PAREY IN BERLIN AND HAMBURG

Berlin SW 61, Lindenstrasse 44/47, Germany

ANIMAL PRODUCTION

JOURNAL OF THE BRITISH SOCIETY OF ANIMAL PRODUCTION

Contents of Volume 3, Part 1, February, 1961

MAHADEVAN, P. & MARPLES, H. J. S. An analysis of the Entebbe herd of Nganda cattle in Uganda.

FRASER, J. D. A comparison of whole milk with buttermilk in the rearing of calves for veal. 1. Rearing and growth.

BARTON, R. A. & KIRTON, A. H. A comparison of whole milk with buttermilk in the rearing of calves for veal. 2. Slaughter and carcass composition data.

SHORTHOSE, W. R. & LAMMING, G. E. The effect of testosterone and oestradiol on growth rate and carcass quality of fattening hoggets.

PRESTON, T. R., CHARLESON, E. B., MACLEOD, N. A., ROSEN, G. D. & VERNON, J. The effect of Hydroxyzine of growth, endocrine, and carcass characteristics of lambs.

BLAXTER, K. L., WAINMAN, F. W. & WILSON, R. S. The regulation of food intake by sheep.

OWEN, J. B. & INGLETON, J. W. A method of collecting faeces from ewes.

HALE, R. W. Heritabilities and genetic correlations of egg production and other characters in a White Wyandotte flock.

WATSON, J. H. The influence of contemporaneity, genetic variation and herd differences on milk yield and fat percentage.

LODGE, G. A. & McPHERSON, R. M. Level of feeding during early life and the subsequent reproductive performance of sows.

BELLIS, D. B. Supplementation of bacon pig rations by aureomycin and copper sulphate.

This journal is a continuation and expansion of the *Proceedings of the British Society of Animal Production* (1944-58) and appears three times per year in February, June and October. The annual subscription is 45s. ($7.50 in U.S.A. and Canada), single parts 17s. 6d. ($2·75 in U.S.A. and Canada) net. Orders and subscriptions should be sent to:—

OLIVER AND BOYD LTD.

Tweeddale Court, 14 High Street, Edinburgh, 1

A GLOSSARY OF SOME TERMS

USED IN THE

OBJECTIVE SCIENCE OF BEHAVIOR

By William S. Verplanck

Provides an empirical vocabulary in the science of human and animal behaviour.

Familiarizes readers with developments in the study of animal behaviour.

Clarifies concepts used by behaviourists and ethologists.

Second Printing **PRICE $1.00**

American Psychological Association

1333 SIXTEENTH STREET, N.W., WASHINGTON 6, D.C., U.S.A.

THE BRITISH TRUST FOR ORNITHOLOGY

is a unique organisation devoted to the encouragement and promotion of

RESEARCH

into the

LIVES, HABITS AND NUMBERS

of

BRITISH BIRDS

Quarterly Journal, *Bird Study* (edited by Dr. J. C. Coulson) free to members: publishes *Bird Migration* (editor Kenneth Williamson) bi-annually, 3s. 6d. each post free; organizes Bird Ringing Scheme, Nest Record Scheme, Census of Heronries; sponsors investigations organized by members; jointly administers Alexander (Reference) Library; Lending Library service; Grants to aid research; Meetings all over the country; 80 Regional Representatives in the British Isles.

Full details of membership from

THE SECRETARY, B.T.O.

2 KING EDWARD STREET, OXFORD

ANIMAL BREEDING ABSTRACTS

The journal of the Commonwealth Bureau of Animal Breeding and Genetics

It covers the world's published research on breeds, breeding, productivity, growth, genetics and reproduction of all farm livestock, poultry, fur bearers and other animals of economic importance, as well as the small laboratory mammals.

Each issue contains a review article on some aspect of current research.

Published quarterly at the beginning of March, June, September and December, at 65/- per annum.

Subscriptions and enquiries to

Commonwealth Agricultural Bureaux

Central Sales, Farnham Royal

Bucks., England

3·4

ANALYSIS OF MATERNAL EFFECTS IN THE INHERITANCE OF BEHAVIOUR

By P. L. BROADHURST

Institute of Psychiatry (Maudsley Hospital), University of London

One of the principal difficulties in the investigation of inheritance in any organism is to guard against possible artefacts arising from the influence of the environment. With mammals there is the additional complication of the maternal environment, any possible effect of which must be carefully excluded. Maternal influence can take many forms: what we are concerned with here are what may be termed strain specific, directional effects by which offspring come to resemble parents in respect of the characteristic being studied. These effects are likely to be confused with genetical ones, and it is particularly important to exclude them in the study of psychological characteristics in the determination of which learned and genetically determined effects are frequently confounded. Thus the resemblance of the behaviour of offspring to that of the parents may be the result of genetical factors, but it is not permissible to assert that such is the case until it has been established that a resemblance is not the result of patterns of behaviour having been otherwise transmitted. Much of the earlier work in psychogenetics, discussed in recent reviews (Fuller & Thompson, 1960; Broadhurst, 1960), is deficient in this respect. This applies particularly to the major selection studies performed by psychologists on the rat, the studies of the inheritance of maze ability (Tryon, 1940; Heron, 1941), of cage activity, (Rundquist, 1933; Brody, 1942), and of emotionality (Hall, 1951). The absence of controls for such effects is especially serious in the last case, since it might be thought that emotional characteristics would be readily learned from parents.

It is the purpose of this paper, therefore, to discuss the manner by which adequate controls for such effects may be instituted and to present the results of the application of such measures in an analysis of the inheritance of emotional reactivity in the domestic rat (*Rattus norvegicus*), using the method of selective breeding.

Maternal Effect

There are two possible times at which a directional maternal influence can arise to mimic inherited effects. The influence may occur during the prenatal period, that is, at conception and during uterine development, or it may be postnatal, that is, during the period from birth to weaning while the young animal is being suckled by the mother. The latter is probably the more sensitive from the point of view of psychological effects, but recent work (Thompson, 1957) has shown that the rodent foetus may also be susceptible to learning *in utero*. In addition, the possibility of more direct physiological, but non-genetical, effects (e.g. hormonal) which may influence behaviour cannot, of course, be ignored.

The necessary control for *postnatal effects* will be considered first. It consists in providing alternative environments for some offspring, then observing whether or not this variation has had a detectable effect on the characteristic being studied. The method employed is the general one of cross-fostering between two or more strains. In the context of the type of selection experiment with which we are principally concerned here, and in which selection is being practised for high and for low expression of a character, two such strains are consequently available. Offspring from, for example, a mother belonging to the high selection line are taken from her at birth and given to a mother from the low selection line for rearing, and *vice versa*. Any postnatal effect can then be detected by comparing the scores of such fostered offspring with those who were not subjected to this change and who were reared throughout by their natural mothers. Three possible outcomes can be envisaged. First, if the offspring resemble the foster-mother more than their natural mother, a postnatal maternal effect can be presumed. Second, if they resemble their natural mother rather than their foster-mother, the absence of any postnatal maternal effect can similarly be presumed, though it should be noted that this does not exclude the possibility of a *prenatal* maternal effect which accounts for the resemblance. Third, if the mean score of the offspring is intermediate between that of natural and foster-mothers a complex situation arises in which either a weak

postnatal effect may be presumed, or, alternatively, for example, a balancing between strong pre- and postnatal effects. Such cases can be resolved only by further analysis involving the study of prenatal effects (see below), which is in any case necessary for a complete specification of directional maternal effects. The cross-fostering procedure is a tedious and time-consuming one; there are, nevertheless, several examples of its use in studies using both rats (Rasmussen, 1939; Thompson & Sontag, 1956; Thompson, 1957) and mice (Butler & Metrakos, 1950; Fredericson, 1952).

The techniques available for the control of *prenatal effects* are less straightforward, and involve certain assumptions about the genetical composition of the strains employed. The usual procedure is to use the method of reciprocal crosses, by which males of one strain are mated with females of a second, and females of the first strain are mated with males of the second, and their progenies compared. In general, it may be said that the expectation is that the offspring of reciprocal crosses between inbred strains should be identical and any large difference between them in the direction of a resemblance to the female parent suggests a maternal effect. This is because the uniform heterozygosity of such F_1's renders them genetically alike; any differences may therefore be attributed to the differential effect of the different intra-uterine environments from conception to parturition provided by the females of the two different strains. It is assumed that the effect of the postnatal maternal effect has already been established or can be discounted.

There are, however, several ways in which genetical effects of one sort or another can disturb this analysis and which, unless care is taken to exclude them, would give results suggesting a genuine prenatal effect of the intra-uterine environment. The first is sex-linkage, as a result of which an F_1 population might resemble the maternal parents more closely than would be expected due to the location on the female sex chromosome of genes determining the given characteristic. In practice this situation would, however, be readily recognized, because it would in principle arise only in one of the F_1 populations; in the other, the reciprocal cross, it would be the males only that would tend to display the maternal characteristics, whereas the females would be more like the fathers.

The phenomenon known as delayed inheritance, in which offspring manifest not their own genotype but that of their female parents, is clearly liable to disturb any analysis of maternal effects using the method of F_1 reciprocal crosses. Fortunately, it appears to be a rare occurrence and limited to major gene effects of the sort unlikely to be met with in the polygenic characteristics usually encountered in mammalian behaviour.

A further condition which might give rise to confusion would be more difficult to detect. If a definite maternal effect were found, there still arises the possibility that it could be due neither to environmental causes arising from the uterine conditions, nor to chromosomal inheritance of the sort we have been discussing and mediated via the cell nucleus of the gametes, but to extra-nuclear or cytoplasmic inheritance. A likely explanation for this type of maternal inheritance lies in the difference in the relative amount of cytoplasmic material contributed by ovum and sperm. Fortunately, a control technique is available for distinguishing between a prenatal maternal effect and one due to cytoplasmic inheritance in such a situation should it arise, and should further analysis be thought desirable. This is the technique of transplanting fertilized ova (McLaren & Michie, 1950; Hall, 1947) which in the present context would involve recovering, from the uterus of a female of one strain, fertilized ova resulting from a mating within that strain and transferring them to the uterus of another female from the opposing strain for further development and birth. The appropriate comparisons with animals from the two strains reared in the normal way should then allow the establishment of the effect of the intra-uterine maternal environment as such, as distinct from any cytoplasmic effects which should be unaffected by the transplantation. The various possibilities for control discussed in this section are illustrated schematically in Table I. Both the first two types of control, cross-fostering for postnatal effects, and reciprocal crossing for prenatal effects, were used in the present experiments.

The Open-field Test

The study which illustrates these procedures relates to the genetical determinants of behaviour in the open-field test of emotionality in the rat (Hall, 1934), a test which is widely used to measure emotional reactivity in rats and mice. It relies principally upon the well-known fear response in these and other species which causes

Table I. Scheme to Show Possible Matings Between Two Lines, High (H) and Low (L), Needed to Display any Maternal Effects.

Type of effect	Type of treatment	Type of mating	Prenatal environment (Uterine)	Postnatal environment (to weaning)
		Female Male		
		H × H	H	L
I Postnatal	Cross-fostering	H × H	H	H
		L × L	L	H
		L × L	L	L
	A. Reciprocal crosses	H × L	H	H
		L × H	L	L
II Prenatal	B. Transplanted Ova	H × H	L	L
		H × H	H	H
		L × L	H	H
		L × L	L	L

Notes: 1. In I and IIB the normal procedure with which each experimental treatment is to be compared is shown on the line below.
2. In IIA and B the possible further variations between pre-and postnatal maternal environment, as given in I, are not shown.

emotional elimination—defecation and urination—and which is mediated via the autonomic nervous system. In addition, the ambulation measure of the animal's activity in the test is obtained; this probably reflects a balancing between the exploratory drive, and the fear response, the extreme form of which is seen in "freezing" (Welker, 1959).

The test has been restandardized for use in this laboratory and some of the difficulties previously associated with its use have thereby been overcome (Broadhurst, 1957, 1958). The defecation and ambulation measures from this variation of the test have reasonable reliability, the coefficients being around 0·80 and 0·75 respectively (Broadhurst, 1960). The arguments for regarding the defecation score from the open-field test as a valid measure of an emotional response have been discussed in detail elsewhere (Broadhurst, 1960).

Method

Apparatus and Test Procedure

The test consists in exposing each animal singly for two minutes at approximately the same hour on four successive days to sound and light fields of uniform intensity in a circular arena 32¾ ins. in diameter with white plywood walls 12½ ins. high. A light metal structure around and above the arena supports both muslin serving as a rough one-way screen and a battery of photographic lamps and loudspeakers which provide the light and "white" noise stimuli having respective intensities at floor level of 165 foot-candles and 78 decibels (ref. 0·0002 dynes/sq. cm.). The number of fecal boluses the rat deposits, and the compartments, marked on the floor and roughly equal in size, through which it passes, constitute the defecation and ambulation scores respectively.

Animals are tested as nearly as possible at 100 days of age. Prior to that time they are reared in a rigidly standardized environment with uniform husbandry. The measures taken to ensure control of these matters of vital concern to any investigation of hereditary differences are described in detail elsewhere (Broadhurst, 1960). Briefly, they feature standardization of diet (MRC No. 41 or 41B and tap water), light/dark cycle (17½/6½ hrs. respectively), size of cage (9 × 9 × 8½ inches high), number of animals per cage (variable until weaning at 21 days of age,

five until 50 days, and three from 50 to 100 days), and amount of handling (three times between birth and open-field testing).

Subjects

All subjects discussed in this paper are descendants of a heterogeneous parental group of 222 albino rats (106 males and 116 females) bred from a remote Wistar stock originally obtained from a dealer. Beginning in 1954 with this parental generation, selection was practised for high and low defecation scores in the open-field test, and has now reached the 14th generation of selection (S_{14}). The closest possible inbreeding (brother × sister mating) is maintained. The present report deals only with those aspects of the results relating to maternal effects and is confined to the generations up to and including S_8.

Cross-fostering

Procedure. The cross-fostering technique for the assessment of postnatal maternal effects was instituted at the beginning of the selection experiment. Cross-fostering whole litters from birth onwards was used. Essential as this procedure is, it was not undertaken lightly, for the minimum interference of the mother rat and her new-born litter is desirable to ensure adequate maternal care.* Advantage was therefore taken of the single routine handling made as soon as possible after birth for the purpose of recording the number and weight of the litter, and providing the mother with nesting material, to effect the exchanges. In only one case was it necessary to delay for as long as one day. The aim throughout was to breed approximately 100 rats of each strain, and to cross-foster one half of these in each generation treated, so that 50 of the offspring of emotionally reactive parents (the high defecating strain) were reared by females of the non-reactive or low defecating strain, the rest being left with their natural mothers, and, conversely, half of the offspring of emotionally non-reactive parents were reared by emotionally reactive females. It was not possible to achieve this aim precisely in each generation (see Tables II and III in the "Results" section) for several reasons; in particular the litters were not born in sufficient numbers at the same time to allow matching for size. The selection of litters for cross-fostering was therefore based on the rule of thumb that alternate litters born in each strain were so treated, provided that there was a litter in the opposing strain available for the exchange. Special care needs to be taken to ensure that the identity of cross-fostered animals is not lost. Since it is difficult to mark new-born pups satisfactorily without resorting to mutilating procedures, the method of exchanging some complete litters and leaving others with their mothers was adopted, rather than attempting to cross-foster a part of each litter. Even this simple procedure involves considerable care and adequate records if confusion is to be avoided. The procedure described above was routinely carried out up to and including the sixth generation (S_6). An alternative procedure would have been to apply the cross-fostering technique at intervals during the progress of selection. This has the disadvantage that the collection of information about any directional maternal effects is protracted, but the advantage that possible changes in the sensitivity of the strains to such effects during the progress of selection might thereby be detected. It is planned, therefore, to resume cross-fostering for one or more generations before selection in these strains is abandoned, in order to check the results reported here.

*An analysis of cross-fostering in relation to fertility and maternal care undertaken for the rats forming one generation only (S_5 parents and S_6 offspring) showed little evidence of any systematic effect of this variable on the following indices: females mated giving birth, fostered, 85·5 per cent. and not fostered, 85·7 per cent.; days from mating to parturition, 24·4, and 24·3 respectively; average size of litters, 8·0, and 7·3; mean birth weight of the pups (g.), 5·4, and 6·2; number of pups born dead, 0, and 1·5 per cent.; number who died before weaning, 25·4 per cent., and 39·7 per cent., and the mean weight at weaning (g.), for males, 30·1, and 31·1, and for females, 27·9, and 30·5.

Results

The results of cross-fostering may be assessed by comparing the open-field test scores of animals from fostered litters with those from litters which were not fostered: the relevant data will be found in Tables II (defecation scores), and III (ambulation scores), and are presented graphically in Figs. 1 and 2 respectively. It will be noted that in each case the scores for male and female rats within the two treatments have been pooled together. While there is definite evidence of sex differences in both the scores, there is little evidence in the results to be presented that there is any *differential* reaction of the two sexes to the cross-fostering treatment which would have precluded this pooling.

Table II. Results of Cross-fostering: Defecation Scores (No. of fecal Boluses per Trial).

Generation	Strain																	
	Emotionally reactive									Emotionally non-reactive								
	Fostered			Not fostered			Both			Fostered			Not fostered			Both		
	n	*M*	SD	*n*	*M*	SD	*n*	*M*	SD	*n*	*M*	SD	*n*	*M*	SD	*n*	*M*	SD
First	47	3·1	1·4	48	3·1	1·4	95	3·1	1·5	48	2·4	1·6	48	2·4	2·0	96	2·4	1·7
Second	55	3·1	1·3	58	2·7	1·5	113	2·9	1·4	36	1·2	1·4	47	0·9	1·3	83	1·0	1·3
Third	46	3·3	0·9	47	3·4	1·1	93	3·4	1·0	45	1·0	1·5	60	1·0	1·1	105	1·0	1·3
Fourth	23	3·5	1·5	37	3·0	1·4	60	3·2	1·5	38	0·2	0·5	42	0·5	1·1	80	0·4	0·9
Fifth	44	3·2	1·1	41	3·3	1·7	85	3·3	1·4	45	0·3	0·7	46	0·1	0·3	91	0·3	0·6
Sixth	44	3·5	1·4	47	3·9	1·4	91	3·7	1·4	44	0·7	1·3	50	1·1	1·9	94	3·7	1·4

Table III. Results of Cross-fostering: Ambulation Scores (No. of Metres Run per Trial).

Generation	Strain																	
	Emotionally reactive									Emotionally non-reactive								
	Fostered			Not fostered			Both			Fostered			Not fostered			Both		
	n	*M*	SD	*n*	*M*	SD	*n*	*M*	SD	*n*	*M*	SD	*n*	*M*	SD	*n*	*M*	SD
First	47	5·8	2·7	48	6·3	2·6	95	6·0	2·7	48	6·1	2·4	48	8·0	2·9	96	7·0	2·8
Second	55	7·6	2·0	58	7·9	4·1	113	7·7	3·3	36	8·9	3·2	47	9·3	2·6	83	9·1	2·9
Third	46	7·8	2·3	47	7·3	2·3	93	7·6	2·3	45	10·6	2·9	60	9·1	2·7	105	9·7	2·9
Fourth	23	8·9	2·7	37	10·0	2·2	60	9·6	2·5	38	10·5	2·5	42	10·6	2·9	80	10·5	2·7
Fifth	44	9·0	2·7	41	9·2	2·9	85	9·1	2·8	45	9·8	2·4	46	10·5	2·3	91	10·1	2·4
Sixth	44	8·7	2·7	47	7·8	3·8	91	8·2	2·8	44	10·0	2·5	50	9·9	3·3	94	9·9	3·3

Inspection of the Tables and Figures shows that while the effect of selection for high and low defecation has had a marked effect upon the defecation scores of the successive generation, as well as influencing the ambulation scores with which they show a slight negative phenotypic correction, there is little evidence of any large or systematic effect of the cross-fostering treatment in the anticipated direction. Statistical analysis by means of analysis of variance (Snedecor, 1956), in general confirms this impression. Tests for homogeneity of variance in the data have routinely been applied to ascertain whether transformations were needed. The results of the analyses are summarized in Table IV.

It should be noted that apart from S_1, they were performed, not on the data for the total number of animals tested in the open-field, but on a sample randomly selected from the total and of the size indicated in column 2. This was done to permit analyses of variance involving three variables, there being two others in the experiment in addition to the cross-fostering treatment, those of strain and sex, (columns 4 and 5 respectively) with which, however, we are not at present primarily concerned. A reduction in the size of all sub-groups to that of the smallest naturally occurring (by virtue of the number of such animals born) was therefore employed. No bias has thereby been introduced into the results; the difference between the mean scores

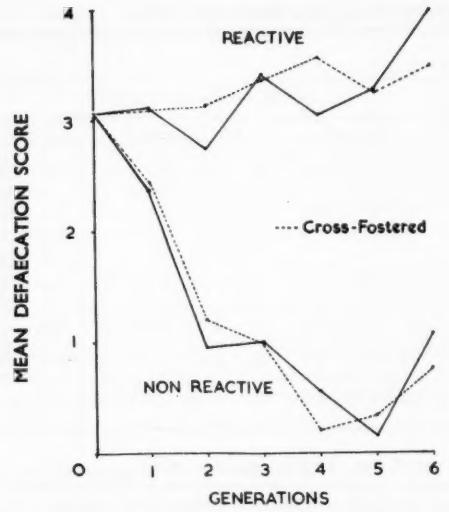


Fig. 1. The graph shows the mean defecation scores per trial of subjects of successive generations of selectively bred rats fostered by own parents (solid line), and by parents of opposing strain (pecked line). Generations, starting with O (Parental) are shown on the abscissa; the ordinate shows the mean number of fecal boluses deposited per trial per day in the open-field test.

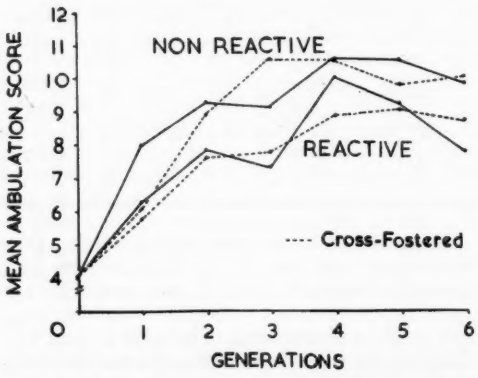


Fig. 2. The graph shows the mean ambulation scores per trial of subjects of successive generations of selectively bred rats fostered by own parents (solid line), and by parents of opposing strain (pecked line). Generations, starting with O (Parental), are shown on the abscissa; the ordinate shows the mean number of metres run per trial per day in the open-field test.

for each sub-group total and for the sample drawn randomly from it were evaluated by means of two-tail *t*-tests and found in every case to be non-significant. In the first generation, a missing score for the single dead animal was supplied to equalize numbers by inserting the mean value for the remainder as an additional score. From the entries in Column 3 of the Table, it will be seen that the variance was frequently inhomogeneous in the defecation data, even after a log transformation of the form $x'=\log(x+1)$. For this reason it is not possible to analyse the data—after the first generation—from both selected strains considered together, and consequently the results shown for the defecation scores from subsequent generations relate to analyses of the two strains considered separately. However, this strategem no longer serves for the non-reactive strain data after the third generation; the inhomogeneity, even after log transformation, again rendering analysis of variance impermissible. No such difficulties were encountered in the analyses of the ambulation data, the results of which are shown in the lower part of the table.

It is clear from Column 6 of the Table that the findings relating to the effects of cross-fostering are generally negative. There are, however, two noteworthy exceptions. The first is the highly significant effect of cross-fostering on the ambulation scores of rats in the first selectively bred generation, and the other to be found is the barely significant ($P=0{\cdot}05$) interaction effect between cross-fostering and sex in the defecation scores of the reactive strain in the third generation. The nature of the first of these effects is clear from Table III. The mean score for the fostered group in each strain in the first generation is below that for the non-fostered. That is to say, there is a general effect displayed by both strains, and not the interaction of the strain and fostering variables expected if nursing by a mother of the opposing strain were having the anticipated directional maternal effect of increasing the resemblance between mother and foster pups—on the one hand, *increasing* the subsequent ambulation scores of reactive strain pups towards the higher level displayed by their non-reactive foster mothers, as well as, on the other hand, decreasing that of non-reactive pups fostered by reactive mothers—the effect actually found in this strain. The support these data lend to an hypothesis of a genuine maternal effect on the open-field test ambulation scores is therefore ambiguous, and it seems that some other explanation is more probable. It may be that complex genetical influences operating in this first generation of

Table IV. Summary of Results of Analyses of Variance of Defecation and Ambulation Scores of Cross-fostered Rats in Open-field Test.

Generation	*N* for analyses	*P* values from:				
		Test of inhomogeneity of variance	Analyses of Variance			
			Main effects			Interactions
			Strain (Reactivity) (R)	Sex (S)	Cross-fostering (F)	
Defecation scores						
First	192	n.s.	n.s.	n.s.	n.s.	R × S, ·001
Second	96	·01*	—	—	—	—
Reactives only	48	n.s.	—	n.s.	n.s.	n.s.
Non-reactives only	48	n.s.*	—	·001	n.s.	n.s.
Third	160	·01*	—	—	—	—
Reactives only	80	n.s.	—	n.s.	n.s.	S × F, ·05
Non-reactives only	80	·05*	—	·001	n.s.	n.s.
Fourth	56	·01*	—	—	—	—
Reactives only	28	n.s.	—	n.s.	n.s.	n.s.
Non-reactives only	28	·01*	—	—	—	—
Fifth	136	·01	—	—	—	—
Reactives only	68	·05	—	n.s.	n.s.	n.s.
Non-reactives only	68	·01	—	—	—	—
Sixth	128	·01	—	—	—	—
Reactives only	64	n.s.	—	n.s.	n.s.	n.s.
Non-reactives only	64	·01	—	—	—	—
Ambulation scores						
First	192	n.s.	·01	·01	·01	n.s.
Second	96	n.s.	n.s.	n.s.	n.s.	R × S, ·01
Third	160	n.s.	·05	n.s.	n.s.	R × S, ·05
Fourth	56	n.s.	n.s.	n.s.	n.s.	n.s.
Fifth	136	n.s.	n.s.	n.s.	n.s.	n.s.
Sixth	128	n.s.	·01	·01	n.s.	n.s.

*=test and any subsequent analyses shown performed on a log transformation of the data.

n.s.=not significant $P > ·05$.

selection have combined to produce the effect found, but it is difficult in this case to see what they could have been, or how they might have operated. An alternative is that it is the fostering procedure itself which has had a dramatic effect in depressing adult ambulation scores. This seems to the writer to carry the concept of maternal deprivation (Bowlby, 1951; O'Connor, 1956) beyond the limits of biological expectation by applying it to animals of the rat's level of development. A further possibility is that the effect is simply a chance determined one of the sort that must occur from time to time in the analyses of large bodies of data. This explanation is the one that the writer inclines towards in the absence of a replication of this part of the experiment.* This view may be thought to be reinforced by the almost complete absence of any other evidence suggestive of directional maternal effects in the ambulation data.

The second noteworthy effect is the minor one occurring among the reactive rats of S_3 and further analysed in Table V, which shows that the difference in defecation scores between sexes among rats not cross-fostered is principally

Table V. Analysis of Interaction of Fostering with Sex in S_3, Reactive Strain Mean Defecation Scores (No. Local Boluses per Trial).

		Treatment	
		Fostered	Not fostered
Sex	Male	3·3 n.s.	3·8
		n.s.	$P<·05$
	Female	3·6 n.s.	3·1

responsible for the significant interaction shown in Table IV. The other difference sbetween the sub-groups are non-significant when evaluated by two-tail *t*-tests, though there is a tendency for the animals fostered (by non-reactive mothers) to respond differently according to sex—the males subsequently displaying lower defecation scores in accordance with an hypothesis of maternal effects, whereas the females become less like their foster mothers, and have higher scores than the non-fostered group. Here again, therefore, the evidence of a maternal effect is ambiguous, though in this case it is altogether weaker as well. In the absence of any suggestion of a similar effect on defecation among other fostered groups, it seems reasonable to assert the absence of any important directional maternal effect on defecation.

*While it is unlikely that it will ever be possible to replicate the early stages of the selection experiment exactly, it is possible to institute a control for the effects of fostering alone, i.e. without cross-fostering between the strains. It is proposed to incorporate this in the resumption of fostering procedures referred to earlier and to be undertaken before the selection experiment is terminated.

Reciprocal Crosses

Procedure. It is perhaps paradoxical that in the type of selective breeding experiment with which we are concerned here it is not possible to institute the control for prenatal maternal environmental effects by reciprocal crossing until a later stage than is possible for the cross-fostering control for postnatal effects. In the first place, it is necessary to wait until sufficient separation has been achieved between the strains in respect of the characteristics being studied to allow the possibility that the two cross-bred or F_1 populations may be demonstrably different in these characteristics. Clearly, the greater the separation between those strains, the greater the likelihood of unequivocal results. In the absence of dominance the expectation is that the scores for the cross-bred population as a whole will lie intermediately between those for the parental strains, P_1 and P_2, from which they are derived, though in the case of a marked degree of dominance, they may be deflected towards one or other of the parental scores, or, in the case of over-dominance (heterosis), transgress the limits defined by those scores, so that the F_1 is greater or less than both P_1 and P_2. The important consideration for our present purposes, however, is that, in the absence of maternal effects, the offspring of both types of reciprocal cross should behave in the same way. The second consideration making for delay before beginning reciprocal crossing with the selected strains is the requirement of the logic of the genetical analysis (see earlier), which presupposes the use of highly inbred strains as the P_1 and P_2. Ideally at least 20 consecutive generations of mating brother with sister are needed to ensure an approach to homozygosity in them; but in pratice five to ten generations will have increased it substantially. As a check on this point the experiment can be repeated using, not selected strains, but two or more others. These should, like the selected strains, differ in the characteristics being studied but also show a higher degree of inbreeding as well.

Crosses between the high and low defecating lines were made reciprocally using animals from the S_6, S_7 and S_8 generations as parents. In addition, the F_1 so generated was in one case (S_8) reciprocally backcrossed to each of the two parental lines, though this was not done primarily for the purpose of analysing maternal effects. The relevant information thus obtained is, however, of interest and will be included in the present report. The parents for breeding each F_1 cross were chosen from the general parental population by virtue of their extreme defecation scores, either high or low, in the open-field test and their proved fertility (in previous breeding for the next generation in the selection experiment). They also represented different litters and consequently the different sublines constituting these populations. The matings were made using a table of random numbers. All parents drawn from the high inbred selection strain had mean defecation scores of 3·5 or more, all those from the low selection line had scores of zero.

Results. The mean scores from the open-field test for the various parental groups will be found in Table VI, along with those for their

Table VI. Results of Reciprocal Crosses: Open-field Test Scores of Parents and Offspring.

Generation	Groups		Cross					Reciprocal				
			a. Reactive females X b. Non-reactive males					a. Non-reactive females X b. reactive males				
			n	Defecation Scores*		Ambulation Scores**		*n*	Defecation Scores		Ambulation Scores	
				M	SD	*M*	SD		*M*	SD	*M*	SD
Sixth	Parents (S_6)	a	3	4·5	0	8·5	2·2	3	0	0	13·0	1·7
		b	3	0	0	10·5	2·9	2	5·5	0	8·7	2·2
	Offspring (F_1)		24(3)***	2·3	1·4	9·6	1·5	20(3)	2·1	1·7	9·4	2·3
Seventh	Parents (S_7)	a	5	3·9	1·5	10·0	1·3	6	0	0	11·2	1·5
		b	4	0	0	9·6	2·3	4	5·8	0·7	8·3	1·5
	Offspring (F_1)		40(5)	3·8	1·4	7·4	1·7	45(6)	3·2	1·9	9·0	1·9
Eighth	Parents (S_8)	a	7	5·6	0·5	8·4	0·8	7	0	0	10·7	3·3
		b	3	0	0	8·5	2·0	3	5·9	0·1	6·2	0·5
	Offspring (F_1)		58(7)	1·9	1·5	9·3	2·3	48(7)	1·2	1·5	9·6	2·2
Backcross to Reactive Strain			a. Inbred females (reactive or non-reactive) X b. Cross bred (F_1) males					a. Cross bred (F_1) females X b. Inbred males (reactive or non-reactive)				
	Parents (S_8 & F_1)	a	5	4·8	0·6	7·7	2·2	5	0·7	0·7	10·4	1·5
		b	5	3·1	1·1	9·1	1·9	5	5·5	0·4	7·7	2·3
	Offspring (B_1)		68(8)	3·3	1·4	7·4	2·0	82(9)	3·1	1·8	7·0	2·6
Backcross to Non-reactive Strain	Parents (S_8 & F_1)	a	3	0	0	13·0	3·2	5	1·5	1·3	9·5	1·8
		b	3	2·8	1·1	8·6	1·2	6	0	0	10·2	2·1
	Offspring (B_2)		48(5)	0·5	1·1	10·4	2·9	72(8)	1·2	1·7	8·6	2·9

Notes: *=No. of boluses deposited per trial.
**=No. of metres run per trial.
***=Figures in brackets indicate the number of litters.

offspring.* Before proceeding to the analysis of the latter scores, it is important to consider whether or not any bias could unintentionally have been introduced into the results by the selection of the parents within the opposing strains. This might have operated by a fortuitous —since the parents of opposing strains were mated randomly—combination of particular parental scores thereby influencing the scores of their offspring. That is to say, if the animals assigned as parents to one type of cross differed systematically from those constituting the parents of the other, then, depending on the direction of the difference, it might be argued that this could have contributed to any found difference (or resemblance) in the scores of their cross-bred offspring. Accordingly, the "mid-parent" score (not shown in the Table) was calculated for each rat in the various groups of offspring by averaging the appropriate two parental values, and the pooled data for both sexes subjected to *t*-tests of the significance of the difference between the relevant means. Considering the defecation scores first, in each case the difference was highly significant, but, with one exception, in the direction opposite to that which would give rise to a spurious directional maternal effect. That is to say, the animals having mothers from the low scoring (non-reactive) strain had higher mean mid-parental values, rather than the lower ones which might have suggested a spurious maternal effect. This rather systematic effect is attributable to the known sex differences in the defecation score; the females scoring lower than the males, as may be seen from Table VI. But the sex difference operated in this case only in the high scoring (reactive) strain; in the low scoring (non-reactive) line there were sufficient parents with zero scores in *both* sexes available for the crosses. Thus the high mother X low father cross inevitably produced higher mid-parent scores than the reciprocal cross, low mother X high father, as the low strain contributed nothing in either case, and differences were in consequence determined completely by the scores of the reactive strain rats which involved the sex difference noted. A similar effect operated in the B_2 backcross (to the non-reactive strain). The exception to this general trend was the B_1 backcross (to the reactive strain) where the mean mid-parental value of the offspring having the inbred strain as mothers was significantly higher than that of the offspring having the cross-breds (F_1) as mothers.

The ambulation scores for the mid-parents determined in the same way are not complicated by a sex difference operating in one strain only as in the defecation scores. In three of the comparisons, S_6 and both backcrosses, there is a difference which is significant at the 5 per cent. level or beyond, in the direction favourable to the display of apparent directional maternal effects in the offspring; in one case, S_7, the difference was also weakly significant but in the opposite direction, and in S_8 there was no significant difference. These preliminary analyses indicate, therefore, that it was not possible to equate our experimental population derived from the reciprocal crosses exactly in the respect of their *parental* scores, and the differences found must be borne in mind in interpreting the results which follow.

The differences between the reciprocal crosses were evaluated as before, sex constituting a second variable in these 2 × 2 analyses of variance. Separate ones were performed for each generation and also for the combined data for the three replications of the reciprocal crosses from the inbred selection strains. A summary of the result will be found in Table VII. It will be seen that these data were generally suitable for the analysis of variance, except in the case of the B_2 defecation scores, where two-tailed *t*-tests were applied to appropriate differences with the results included in the table.

The sex difference (Column 6) is ubiquitous, and in each case is in the direction to be expected from previous experience of this test, that is, males exceed females in amount of defecation, but females ambulate more. It is noteworthy that this sex difference, originally found in unselected populations (Broadhurst, 1957) and which had become attenuated, and even in some cases reversed during selection (Broadhurst, 1958, 1960), has again become fully evident in these cross-bred populations. There is little suggestion that this striking sex difference in any way interacts (Column 7) with the variable of maternal strain which is our present concern. In only one case—the ambulation score for the sixth generation cross—is the interaction effect weakly significant. Study of this interaction in-

*For reasons unconnected with the present discussion and otherwise irrelevant to it, the parents from the S_7 group only were tested in the open field under a higher noise level (87 decibels). This noise level was consequently used in testing their F_1 offspring, so that the variation in conditions would not vitiate any comparisons between parents and offspring.

Table VII. Summary Results of Analyses of Variance of Defecation and Ambulation Scores in Open-field Test of Reciprocal Crosses.

Generation	*n* for analyses	Score	*P* values from:			
				Analyses of variance		
				Main effects		
			Test of inhomogeneity of variance	Strain of mother	Sex	Interaction
F_1 of Sixth (S_6)	44	D	n.s.	n.s.	·05	n.s.
		A	n.s.	n.s.	·05	·05
F_1 of Seventh (S_7)	85	D	n.s.	n.s.	·001	n.s.
		A	n.s.	·001	·001	n.s.
F_1 of Eighth (S_8)	106	D	n.s.	·001	·001	n.s.
		A	n.s.	n.s.	·001	n.s.
F_1 of S_6 to S_8 combined	235	D	n.s.	n.s.	·001	n.s.
		A	n.s.	·05	·001	n.s.
Backcross (B_1)	150	D	·05	n.s.	·001	n.s.
		A	n.s.	n.s.	·01	n.s.
Backcross (B_2)	120	D	·01	— (n.s.)*	— (·05)*	—
		A	n.s.	·05	·001	n.s.

Notes: D=Defecation score in no. of boluses deposited per trial.
A=Ambulation scores in no. of metres run per trial.
*=Derived from two-tail *t*-tests.

dicates that it reflects the fact that a prominent sex difference ($P<·01$) among rats reared by non-reactive mothers does not appear among those reared by reactive ones. There is no strain difference as such within either sex. These results suggest that we can dismiss the sex difference from consideration in the present context.

The Table shows some significant differences due to strain of mother (Column 5); in each case they are in the direction of a greater resemblance of offspring to mother, i.e. directional maternal effects, as may be seen from Table VI. Among the defecation data, there is a consistent trend in favour of such a maternal effect, which, however, only reaches significance in the offspring of S_8. In the pooled data for the three replications the effect again fails to reach significance. These findings suggest therefore that the effect is weak, though it will be remembered that any possible influence due to the choice of parents may have operated against it. However, since in the case of the B_2 backcross where this consideration does not hold, and indeed the reverse may have been the case, the difference is the smallest found, it suggests that the choice of the parents as reflected in their own scores, had little influence on the maternal effect. The ambulation data show a more pronounced directional maternal effect in certain cases, though with less over all consistency. Thus, in two cases (S_6 and B_1), the trend, though non-significant, is in the opposite direction. However, the highly significant effect on S_7 is supported by the weakly significant effects in the data for the three replications pooled, and for the backcross (B_2) to the non-reactive (high ambulating) strain. Here again, the parental scores do not appear to have had any obvious influence; they may have contributed to the effect found in the backcross, but any anticipated influence on the S_7 offspring would have attenuated the difference found. Thus the evidence again suggests that the directional maternal effect revealed is a weak one.

Discussion and Conclusions

The results presented show little evidence of any marked pre- or postnatal directional maternal effects on the open-field test scores of the Maudsley strains of rats selectively bred for emotional reactivity. It is not possible to conclude that there has been no maternal influence whatsoever in determining the individual differ-

ences in the behaviour measured, but merely that it has not shown up strongly as a major source of variability under circumstances judged favourable for its occurrence. This conclusion is more certain in relation to postnatal rather than prenatal effects, and in relation to defecation rather than to ambulation. It is tempting to speculate why this should be the case, but probably unprofitable until the basis for such speculation is more secure. It should also be remembered that the lack of complete homozygosity in our selected strains makes the conclusions based on reciprocal crosses between them less certain. Fortunately, some other data are available from an experiment (Broadhurst, 1960) using the method of diallel crossing (Hayman, 1954b; Jinks, 1954) in which six inbred lines, one of which was the low defecating selection line also used here, were reciprocally crossed in every possible combination, and the experiment replicated so that 595 subjects were eventually reared, and tested in the open field, in the standardized manner described. The two diallel tables thus generated for each of the two open-field test scores were then analysed to obtain various genetical parameters, and were also subject to analyses of variance (Hayman, 1954a). In neither score was the mean variance attributable to reciprocal differences significant when tested against the appropriate residual term. This incidental result from a large scale experiment the majority of the subjects of which were representatives of, or cross-bred from, highly inbred strains strongly supports the suggestion that prenatal maternal effects are unimportant in the behaviour of the subjects studied in the present experiments. Nothing comparable to the curious *negative* maternal effect revealed in Broadhurst & Jinks (1961) reanalysis of Brody's reciprocal cross data (1942) for activity has been found and certainly the indication of maternal effects are generally insufficiently definite to warrant further analysis designed to exclude the possibility of maternal or cytoplasmic inheritance of them. The entire absence of any indications of an interaction of reciprocal differences with the strong sex differences found similarly argues against the possibility of any important sex linkage among the genes determining the expression of the traits studied.

It is fortunate that it has been possible to arrive at this conclusion, since it implies that the results from Hall's (1951) selection experiment may not have been vitiated by the absence of any control for maternal effects. In the present experiment, which constitutes a replication of Hall's work, though using a different foundation population, the progress of selection has been similar, and inter-strain differences, both behavioural and physiological, have arisen which resemble those reported by Hall and his coworkers (Broadhurst, 1961). It is not possible to extend this conclusion to the other selection experiments in psychogenetics, but it can be said that it renders the possibility of major maternal effects having operated in them less likely, since there are grounds for thinking that emotional elimination might be especially sensitive to such influences.

The methods for the detection of strain specific, directional maternal effects employed in the experiments described above have a wider applicability than is perhaps suggested by their use in connection with a selection experiment of the sort described. As has been emphasized earlier, they can be applied to any comparison of inter-strain differences in mammals, not necessarily strains created by selection. The scheme indicated in Table I is applicable generally. While it is at present rare to find much concern with controls for possible artefacts of this sort among workers in comparative psychogenetics, reciprocal crossing and, less frequently, cross-fostering are sometimes reported, but not both together. It is to be hoped that, with the resurgence of interest in this field of research (Fuller & Thompson, 1960), adequate consideration of the possibility of maternal influences on behaviour will become routine.

Summary

The necessity for the determination of directional maternal effects in experiments on the inheritance of behavioural characteristics in mammals is stressed, and the available procedures for doing so are discussed and illustrated from studies of the inheritance of emotional reactivity in the rat as measured in the open-field test. Cross-fostering of litters between lines in an experiment in which selection for extremes of emotional elimination was practised was used to test for postnatal maternal effects, and reciprocal crossing between the lines for prenatal effects. There is little evidence in favour of the operation of maternal influences upon these characteristics at either stage in development.

Acknowledgments

I am indebted to the staff and students of the Animal Psychology Laboratory, especially Mr. K. B. Wraight, for assistance in testing the experimental subjects, and to Miss S. B. Parsons, for computational help. Dr. A. G. Dickinson kindly read the MS and made several helpful suggestions. The Ford Foundation gave financial support.

REFERENCES

Bowlby, J. (1951). *Maternal care and mental health.* WHO Monogr. Ser., 2, Geneva.

Brody, Elizabeth G. (1942). Genetic basis of spontaneous activity in the albino rat. *Comp. Psychol. Monogr.*, **15,** no. 5, 1-24.

Broadhurst, P. L. (1957). Determinants of emotionality in the rats: I. Situational factors. *Brit. J. Psychol.*, **48,** 1-12.

Broadhurst, P. L. (1958). Determinants of emotionality in the rat: II. Antecedent factors. *Brit. J. Psychol.*, **49,** 12-20.

Broadhurst, P. L. (1960). Experiments in psychogenetics: Applications of biometrical genetics to the inheritance of behaviour, in H. J. Eysenck (Ed.) *Experiments in personality*: Vol. I, *Psychogenetics and psychopharmacology*. London: Routledge & Kegan Paul. Pp. 1-102.

Broadhurst, P. L. (1961). Some effects of manipulating thyroid output on open-field test behaviour in the rat. *Anim. Behav.*, **9,** 113 (Abstract).

Broadhurst, P. L. & Jinks, J. L. (1961). Biometrical genetics and behavior: reanalysis of published data. *Psychol. Bull.* (in press).

Butler, L. & Metrakos, J. D. (1950). A study of size inheritance in the house mouse: I. The effect of the milk source. *Canad. J. Res., Section D,* **28,** 16-34.

Fredericson, E. (1952). Reciprocal fostering of two inbred mouse strains and its effect on the modification of inherited aggressive behavior. *Amer. Psychologist,* **7,** 241-242 (Abstract).

Fuller, J. L. & Thompson, W. R. (1960). *Behavior genetics.* New York: Wiley.

Hall, C. S. (1934). Emotional behaviour in the rat: I. Defecation and urination as measures of indivudal differences in emotionality. *J. Comp. Psychol.*, **18,** 385-403.

Hall, C. S. (1947). Genetic differences in fatal audiogenic seizures between inbred strains of house mice. *J. Hered.*, **18,** 3-6.

Hall, C. S. (1951). The geneticis of behavior, in S. S. Stevens (Ed.) *Handbook of experimental psychology*. New York: Wiley. Pp. 304-329.

Hayman, B. I. (1954a). The analysis of variance of diallel crosses. *Biometrics,* **10,** 235-244.

Hayman, B. I. (1954b). The theory and analysis of diallel crosses. *Genetics,* **39,** 789-809.

Heron, W. T. (1941). The inheritance of brightness and dullness in maze learning ability in the rat. *J. genet. Psychol.*, **59,** 41-49.

Jinks, J. L. (1954). The analysis of heritable variation in a diallel cross of *Nicotiana rustica* varieties. *Genetics,* **39,** 767-788.

McLaren, Anne & Michie, D. (1956). Studies on the transfer of fertilized mouse eggs to uterine foster-mothers: I. Factors affecting the implantation and survival of native and transferred eggs. *J. exp. Biol.*, **33,** 394-416.

O'Connor, N. (1956). The evidence for the permanently disturbing effects of mother child separation. *Acta psychol.*, **12,** 174-191.

Rasmussen, E. W. (1939). Wildness in rats: heredity or environment? *Acta psychol.*, **4,** 295-304.

Rundquist, E. A. (1933). Inheritance of spontaneous activity in rats. *J. comp. Psychol.*, **16,** 415-438.

Snedecor, G. W. (1956). *Statistical methods applied to experiments in agriculture and biology* (5th ed.). Ames, Iowa: Iowa State College Press.

Thompson, W. D., Jnr. & Sontag, L. W. (1956). Behavioral effects in the offspring of rats subjected to audiogenic seizure during the gestational period. *J. comp. physiol. Psychol.*, **49,** 454-456.

Thompson, W. R. (1957). Influence of prenatal maternal anxiety on emotionality in young rats. *Science,* **125,** 698-699.

Tryon, R. C. (1940). Genetic differences in maze-learning ability in rats. *Yearb. nat. Soc. Stud. Educ.*, **39,** 111-119.

Welker, W. I. (1959). Escape, exploratory and food-seeking responses of rats in a novel situation. *J. comp. physiol. Psychol.*, **52,** 106-111.

Accepted for publication 13*th October*, 1960.

SWIMMING AND REACTION TO ELECTRIC SHOCK IN TWO SUBSPECIES OF DEERMICE (*Peromyscus maniculatus*) DURING DEVELOPMENT*

By JOHN A. KING

Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine

Peromyscus maniculatus is the most widely distributed species of *Peromyscus* in North America (Hall & Kelson, 1959). Among its 60 or more geographic races are *P. m. gracilis* and *P. m. bairdii*; members of a racial circle extending about the Great Lakes basin. *P. m. gracilis* occupies the forested regions of the northern Great Lakes states, and *P. m. bairdii* is found in the grasslands of the midwestern states. In northern Michigan and New York their ranges overlap, but they usually are isolated ecologically (Hooper, 1942; Barbahenn & New, 1957). The two races are morphologically distinct (McIntosh, 1955), and many behavioural differences have been recorded (Foster, 1959; Harris, 1952; Horner, 1954). Also, in development, *P. m. bairdii* matures physically and behaviourally more rapidly than *P. m. gracilis* (Svihla, 1932, 1935; King, 1958). The purpose of the present study is to describe the development of two types of postnatal behaviour in both subspecies in an effort to examine the factors influencing their behaviour. A description of the development of swimming and reaction to electric shock is presented for groups of both subspecies studied throughout their development (longitudinal) and groups examined at one age (cross-sectional). The swimming and electric shock situations were used because the aversive stimuli of water and shock motivated the mice to respond. In the absence of adequate stimuli, young mice frequently fail to exhibit observable behaviour within a short test period. The development of the swimming response was primarily selected to reveal differences in the rate of motor development, because there was no reason to suspect adult differences in the swimming ability of both subspecies. The development of subspecific differences in response to electric shock (Foster, 1959) was examined in order to reveal experiental factors which may be responsible for the behavioural divergence.

*This study was supported by Research Grant M-123 of the National Institute of Mental Health, Public Health Service. The author is grateful to Nancy J. Shea and Patricia F. Waller for their thoughtful assistance in collecting and analysing the data.

Method

The mice came from colonies of *P. m. bairdii* and *P. m. gracilis* which had been bred in the laboratory since 1948. The colony was examined for new-born litters once or twice each day. All litters were reduced to four young on the third or fifth day after birth. Individuals of each litter were numbered by removing one of the four toes on the right forefoot prior to their first test. At 21 days of age the mice were weaned, and the siblings were placed together in wooden cages 6 in. wide, 12 in. long, and 6 in. high. Litters were assigned to longitudinal or cross-sectional groups as units. Two individuals from each litter were given swimming tests, and two were given escape from electric shock tests.

Ten litters of each subspecies were tested every other day from 10 to 29 days of age; one longitudinal group of five litters (*a*) began on the tenth day of age, and another longitudinal group of five litters (*b*) began on the eleventh day. (Tables I and II). Twenty-five litters were assigned to five cross-sectional age groups of five litters each. Each group was tested at one of five ages: 13, 15, 18, 20 and 25 days of age. All mice were given both swimming and escape-shock

Table I. Number of Litters and Individuals in Each Group of *P.m. gracilis*. (The same numbers were used for ***P.m. bairdii***).

	No. of litters	No. of individuals
Longitudinal	10	
Water		20
Shock		20
Cross-sectional	25	
Water		50
Shock		50
70 day controls	5	20
Totals	40	160

PLATE V

Fig. 1. Swimming test apparatus. Mice enter water at end of plastic cylinder and swim to screen platform across the tub.

PLATE VI

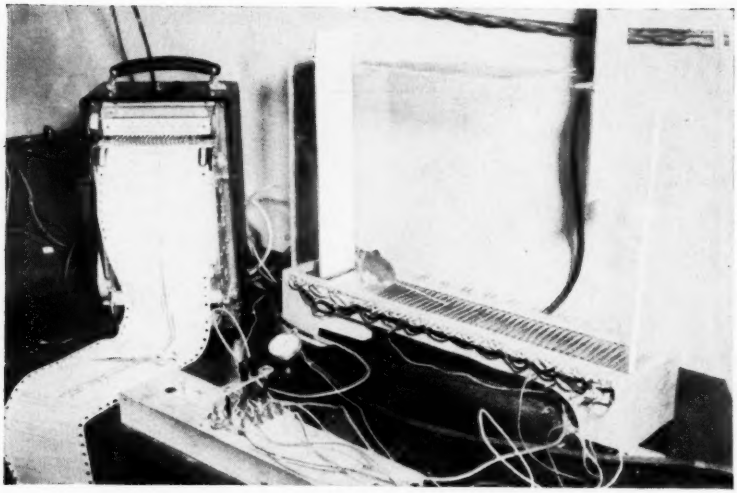


Fig. 2. Electric shock apparatus. Mice run across electrified grid to insulated pan (shown with mouse on it) at far end of enclosure. The door immediately behind pan was raised in the second of each pair of trials. Recording apparatus consists of microswitch keyboard and Esterline-Angus Recorder.

Table II. Age of Testing (Indicated by X) of All Groups of Mice of Both Subspecies.

Group	10	12	14	16	18	20	22	24	26	28	30	70
Long. A*	x	x	x	x	x	x	x	x	x	x		x
Long. B*		x	x	x	x	x	x	x	x	x	x	x
X-Sect. 13 day		x										x
X-Sect. 15 day				x								x
X-Sect. 18 day					x							x
X-Sect. 20 day						x						x
X-Sect. 25 day									x			x
Control												x

*Longitudinal A began tests at 10 days of age and were tested on alternate days thereafter. Longitudinal B at 11 days of age.

tests again at 70 days of age. A 70 day old control group consisting of five litters of four mice each was also given both tests. A total of 320 mice from 80 litters was used.

Swimming Test

Apparatus. The apparatus was constructed to test the swimming performance of mice across 16 inches of water to a ¼ inch mesh screen platform standing in the water (Fig. 1). The water was in a washtub 20 inches square, with water 4 inches deep, and held at a temperature between 27° and 30°C. The mice were dropped 2 inches into the water by releasing a trapdoor at the bottom of a hollow plastic cylinder which was fastened to one side of the tub. The mice could climb out of the water onto a screen platform rising vertically 4 inches above the water on the opposite side of the tub. The platform had a flat top 4 inches square.

Procedure. The mouse was placed in the cylinder for about 15 seconds before being released into the water. There were two trials of 1 minute duration in each sequence. At the end of the first trial, the mouse was removed from the water or screen platform and replaced in the cylinder. After the second trial the mouse was returned to its holding cage. Longitudinal mice were given a two-trial sequence of tests every other day. Cross-sectional mice were given another pair of trials after 10-15 minutes in the holding cage and the procedure was repeated until they had as many trials as the longitudinal mice at the same age as the cross-sectional group. The principal records used were the time it took a mouse to reach the screen platform after being dropped into the water (swimming latency) and the longest continuous period of time a mouse remained on top of the screen platform after it had reached the top. These measures were recorded on an Esterline-Angus Operation Recorder by manually operating a microswitch keyboard. At 70 days of age all groups were given two trials in the swimming apparatus.

Shock Test

Apparatus. The test was designed to measure a mouse's response to electric shock in an escape situation. A Plexiglas enclosure, 20·5 inches long, 3 inches wide and 12 inches high, was placed on a stainless steel grid constructed of ⅛ inch diameter bars ¼ inch apart (Fig. 2). A continuous electric current was supplied to the grid by a transformer delivering 195 volts through a 4·7 megohm resistor in series with the mouse. The mice could escape the shock by sitting on a flat aluminium pan 3 inches square, which fitted over the grid 2 inches from the end of the enclosure. The weight of a mouse depressed the pan and activated a microswitch, which recorded its frequency and duration on the pan. Two guillotine doors of masonite closed off sections at both ends of the enclosure. One door 3 inches from one end of the enclosure formed the starting chamber, and the other door 2 inches from the opposite end formed a back to the edge of the aluminium pan. Raising the starting door activated a microswitch which indicated the start of the trial.

Procedure. The mouse was placed in the starting chamber 15 seconds prior to the raising of

the door and the onset of shock. Electric current to the grid was supplied simultaneously with raising the door. Shock was continuous for 1 minute, during which period the mouse was free to move about on the grid or remain on the pan, where it escaped shock. During the first of two trials, the door behind the pan was in place, thus preventing the mouse from running over the pan to the grid beyond. After the first trial, the mouse was gently forced back to the starting chamber, the door behind the pan was raised, and the shock again presented for a minute beginning simultaneously with releasing the mouse from the starting chamber.

Longitudinal mice were given the test every other day, and cross-sectional mice received the two trials at intervals of approximately 15 minutes until they had accumulated the same number of trials as the longitudinal mice at the same age. This procedure provided an estimation of the effect of prior experience. The automatically recorded measures made on the Esterline-Angus Recorder were latency to the pan, duration on the pan, and frequency on the pan. The measure used in this report was the longest continuous time a mouse spent on the pan during each trial. At 70 days of age all groups were given four trials in the shock apparatus, two with the partition behind the pan down, and two with the partition removed.

Analysis of variance was applied to most measures; however, the lack of normal distributions and the unsuitability of most transformations make the statistical tests approximate. The probability levels were doubled in an effort to make significant differences more reliable (Lindquist, 1953). The Mann-Whitney U test was used where subspecies-treatment interactions were unnecessary.

Results

Swimming Test

The behaviour of 10 to 14 day old *Peromyscus* upon entry into water usually consisted of coordinated swimming motions, although a few mice floated motionless in the water. *Bairdii* at 10 days kept their noses out of the water, but several *gracilis* arched their backs until their noses became submerged and they soon suffered anoxia. At 10 days, swimming lacked direction, and the mice frequently swam in circles. Those reaching the side of the tub often pawed the sides at one place. A few mice occasionally contacted the platform and clung to it while remaining entirely or partially submerged. Swimming strength increased with age, and the mice often swam along the side of the tub until they reached the platform. After the opening of the eyes, which occurs at different ages in the two subspecies, the mice usually swam directly to the platform and climbed to the top.

Swimming Latency. Longitudinal and cross-sectional groups in both subspecies showed a significant decrease in mean latency with age (Fig. 3 and Table III). Means of the 20 longitudinal mice in each subspecies generally followed the mean established by the cross-sectional groups. The similarity of the means in longitudinal and cross-sectional groups indicates that swimming performance reflects the maturational level of the mouse rather than swimming experience. Although the first and last trial of the cross-sectional groups differed to some extent, the pattern was not consistent. *Bairdii* swam faster during the first trials at 13 and 15 days, while *gracilis* swam slower on the first trial than on the last trial at these ages. At later ages, the relationship between the first and last trial was reversed in both subspecies. Random fluctuations probably accounted for this reversal, since the differences were not significant ($F=1{\cdot}10$; $p>{\cdot}20$).

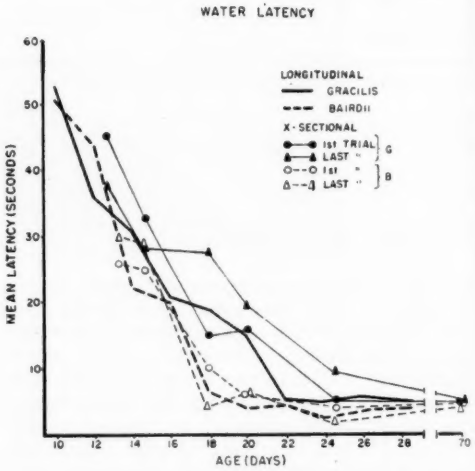


Fig. 3. Water latency scores. The mean amount of time taken by each group to swim across tub to platform. Longitudinal groups are represented by the mean of the two trials given each day. Cross-sectional groups for each age are represented by only their first and last trials.

The subspecific differences illustrated in Fig. 3 showed that *gracilis* reached their asymp-

Table III. F Ratios and Probabilities from Water and Shock Tests.

Test and group	Sub-species	Age	Inter-action
Swim latency			
Longitudinal	5·03	50·70***	2·66
Cross-sectional			
First trial	7·93**	16·18***	·38
Last trial	22·46***	19·31***	4·16**
Duration on platform			
Longitudinal	21·22**	478·76***	1·39
Cross-sectional			
First trial	7·67**	23·76***	·21
Last trial	16·38***	18·24***	1·18
Duration on pan-shock			
Longitudinal	101·13***	34·34***	30·39***
Cross-sectional			
First trial	1·96	1·39	12·56***
Last trial	140·01***	11·56	·69

**<·02; ***P<·002

totic level about four days later than *bairdii* in the longitudinal groups. The difference between subspecies in the longitudinal groups was not significant. However, there were significant subspecific differences in cross-sectional groups for both the first and last trials (Table III). Swimming latency of *gracilis* decreased at a different rate from that of *bairdii* as the mice matured. The short latencies of *bairdii* at earlier ages indicate a more rapid maturation of their physical and locomotor abilities than is the case with *gracilis*.

Duration on Top of Platform. Longitudinal and cross-sectional groups of *bairdii* spent longer continuous periods on top of the platform than did *gracilis* (Fig. 4). The subspecific and age differences were significant in both the first and the last trials (Table III). The lack of a significant subspecies-age interaction indicates that the change in performance during development was similar in both subspecies. The age difference represents climbing skill to a certain extent, because the 20-30 day old mice could climb up the screen faster than the 10-16 day old mice. The subspecific differences on top of the platform resulted from the tendency of *gracilis* to leave the platform, climb about its sides, and occasionally re-enter the water deliberately.

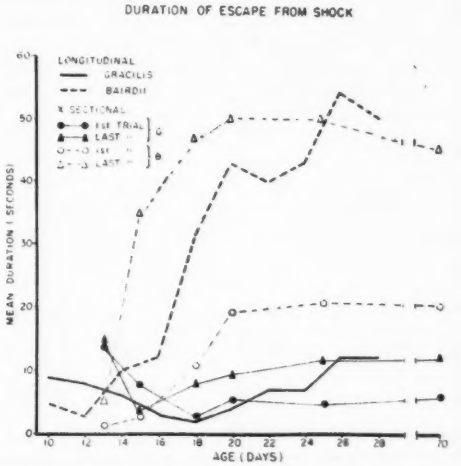


Fig. 5. Mean longest continuous time all groups spent on safe pan on an electrified grid without going back onto grid. Scores are with the door behind the pan raised.

70 *Day Tests.* Swimming latencies of all groups of mice at 70 days of age plus a naive control group were essentially alike with respect to age of the early experience, amount of early experience in the apparatus, subspecies, and differences between first and last trials (Table IV). Most adult mice were capable swimmers, and they quickly reached the platform after entering the water.

The longest continuous time spent on top of the platform was not significantly different for any of the age groups (Table IV) indicating no effect of previous experience. At 70 days of age, *bairdii* still spent a significantly longer period of time on the platform ($p<·001$, Mann-Whitney U) than did *gracilis*. Both subspecies also remained on the top of the platform longer during the last trial than during the first trial ($p<·001$, Mann-Whitney U).

Shock Test

When the young were first exposed to an electric shock, they squeaked and scrambled

Table IV. Mean Test Scores in Seconds of First and Last Trials of All Groups of Mice at 70 days of Age.

	Age	Swim latency		Swim duration		Shock duration		
		First	Last	First	Last	First	Last	Diff.
Bairdii	13	5·5	3·9	41·1	52·7	12·5	41·2	28·7
	15	3·2	3·4	36·6	47·6	20·4	51·3	30·9
	18	5·6	5·1	45·4	52·4	28·6	50·2	21·6
	20	4·2	3·2	42·8	47·7	20·8	43·9	23·1
	25	4·1	3·6	39·9	49·6	19·4	45·9	26·5
	Longit.	6·7	5·6	40·2	49·5	20·6	40·9	20·3
	Control	3·7	3·4	35·9	48·2	14·8	45·0	30·2
Gracilis	13	4·5	3·8	34·8	38·4	7·8	18·4	10·6
	15	4·1	7·1	29·0	37·1	5·0	13·9	8·9
	18	3·2	4·1	36·2	41·0	5·2	9·1	3·9
	20	6·3	3·2	33·0	37·4	5·9	10·6	4·7
	25	5·1	3·6	31·1	39·6	4·7	8·6	3·9
	Longit.	5·2	4·4	33·8	36·8	8·9	12·4	3·5
	Control	5·4	9·2	23·0	37·1	4·2	14·0	9·8

over the grid until they encountered the end or sides of the enclosure, which they actively pawed. The continuation of the shock usually kept them in motion until they reached the safe aluminium pan. With the door at the end of the pan down, the mice stopped on the pan and made no further attempt to move. With the door at the far end of the safe pan up, most young mice crawled across the pan to the grid on the other side and back on the pan again. As the mice became more capable of locomotion, their response to shock was violent and they often ran across the pan without stopping. At later ages, each subspecies made qualitatively different responses to the situation.

Duration on Pan. The longest continuous time *bairdii* spent on the safe pan, increased with age, while the performance of *gracilis* changed little with age (Fig. 5). The longitudinal curves show that from 10 to 14 days *gracilis* spent more time on the pan than *bairdii*, probably because of the slower locomotor development of *gracilis*. The more mature *bairdii* crawled across the pan and, thus, spent less time on it. At 14 days, the longitudinal curves cross and subsequently become farther apart, illustrating the tendency of *bairdii* to remain on the pan. There is a significant difference between subspecies, between ages, and in the subspecies-age interaction (Table III).

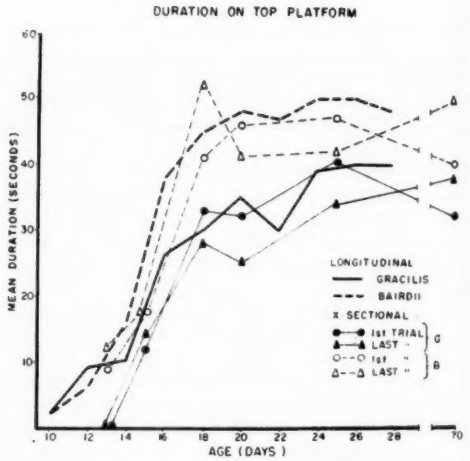


Fig. 4. Mean longest continuous time all groups of mice spent on top of the screen platform after leaving the water.

Subspecific differences were easily observed. *Bairdii* sat on the pan and often groomed themselves or nosed the sides of the enclosure. They rarely froze. *Gracilis* sat on the pan a few seconds, nosed the sides of the enclosure, then extended their heads out over the grid with their ears cocked, and finally ran back onto the grid. Once on the grid again, they leapt about and then ran directly to the pan for a few seconds. This behaviour of *gracilis* resulted in several short periods on the safe pan rather than long continuous periods which were exhibited by *bairdii*. *Gracilis* also spent less total time on the pan than *bairdii*.

The cross-sectional data are more reliable indexes of maturation than the longitudinal data, which confound experience with age. The first trial in the cross-sectional groups demonstrates the response of mice without any prior experience. In general, *gracilis's* response in the first trial was similar among all cross-sectional and longitudinal groups and was also similar to the last trial. The longest record for the cross-sectional *gracilis* was at 13 days of age, when they were not sufficiently mature to run or leap about in the apparatus. The first trial of *bairdii* showed an increase in amount of time spent on the pan with age. No significant differences were found between subspecies or in age on the first trial. A significant subspecies-age interaction ($F = 12{\cdot}56$; $p < {\cdot}002$) indicates that the response of each subspecies differed as the mice matured.

The last trial of *bairdii* in the cross-sectional groups demonstrated that they spent more time on the safe pan as a result of their experience in the apparatus. Apparently three trials at 15 days

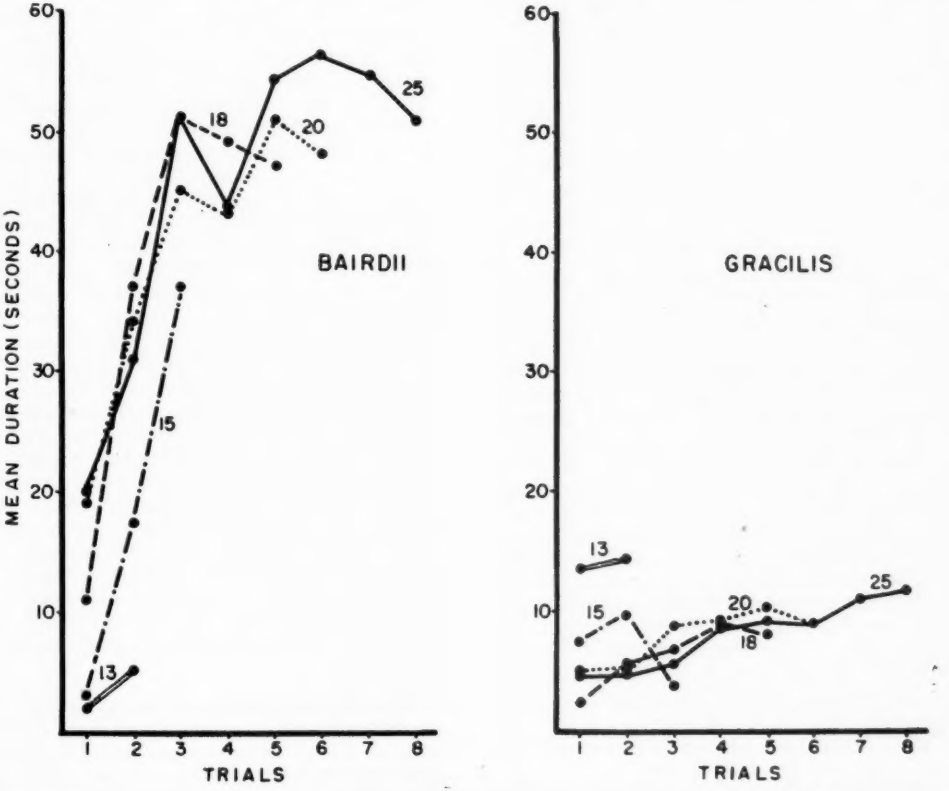


Fig. 6. Mean longest continuous time cross-sectional groups spent on safe pan at each trial of the age group designated by numbers in the figure. Cross-sectional groups received the same number of trials as longitudinal groups of comparable ages.

and older (Fig. 6) provided sufficient experience to improve the performance of *bairdii*. The last trial of the cross-sectional groups was consistently of longer duration than the longitudinal groups, which had received the same number of trials at each age. *Bairdii* spent significantly longer continuous periods on the pan during the last trial than *gracilis*. Performance changed significantly with age. The subspecies-age interaction was not significant. Other measurements in this situation, such as frequency on the safe pan, and total time on the pan, for both the first (partition behind pan lowered) and second test (partition raised) showed similar subspecies and age differences.

70 Day Tests. At 70 days of age all longitudinal and cross-sectional groups and a naive control group were given four trials in order to test the effect of previous experience on later performance. The results of the mean longest continuous time spent on the pan in the second test are presented in Table IV. Neither *bairdii* nor *gracilis* showed consistent differences among the groups resulting from their early experience. Subspecific differences persisted. On both the first and last trials, *bairdii* spent significantly more time on the pan than *gracilis* ($p<\cdot001$, Mann-Whitney U).

Discussion

The geographic separation and ecologic divergence of *P. m. gracilis* into a forest environment and *P. m. bairdii* into a grassland environment has brought about morphological, developmental, and behavioural differences in the evolution of the two subspecies. Morphological differences appear early in postnatal development. Behavioural differences also occur early in development. Some behavioural differences appear to be caused by differences in maturation rates, which disappear in the mature mice. Other differences appear to be genetic, because they emerge early and remain essentially the same throughout the life of the mice, regardless of experience. Still other differences between the behaviour of the two subspecies are those which appear early in development, but are reinforced by experience and increase in magnitude with age. The initial genetic characteristics of each subspecies appear to be reinforced by the animals' experiences and are canalized into the adult patterns they later exhibit.

Subspecific differences in swimming latency appear about 15 or 16 days of age, when *bairdii* begins to reach the platform before *gracilis*, indicating a more rapid maturation of motor development in *bairdii*. When *gracilis* is 21 to 22 days old, its performance matches that of *bairdii*. No differences were recorded in swimming latency after 22 days of age. Prior swimming experience had little effect on this measure as indicated by the similarity of performance in the longitudinal groups and the first trial of the cross-sectional groups. The last trials also failed to reveal any consistent change from the first trials. Although *gracilis* reduced its swimming latency at 13 and 15 days after previous experience in the water, their longer latencies on the last trials at 18 days and after indicated that the effect of experience was not significant. Swimming latency thus appears to be a measure of maturation, unaffected by experience or genetic differences in behaviour.

In contrast to swimming latency, the longest continuous duration of time spent on top of the screen platform appeared to measure subspecific or genetic differences which persisted throughout life after they first emerged. The genetic expression of this behaviour was affected by experience, but this experiment did not reveal the age when the experience was most effective. Until 28 days of age, the cross-sectional groups did not differ significantly from the longitudinal groups or from the first to the last trial. At 70 days of age, however, all groups spent significantly more time on top of the platform during the last trial than they did during the first trial. The change in performance from the first trial to the last trial between 28 and 70 days of age suggests that the mice developed the capacity to modify their behaviour in this situation. Both subspecies changed their performance with the accumulation of experience, but *gracilis* did not reach *bairdii's* level of performance. *Bairdii* tended to inhibit gross locomotor activity while *gracilis* was more inclined to continue moving about on the platform after it had escaped from the water. This difference in the behaviour of the two subspecies on the platform suggests genetic differences which become modified in a similar fashion in both subspecies by the same type of experiences.

The longest continuous time the mice spent on the safe pan in an electrified field revealed genetic differences which were differentially modified by the experiences of each subspecies. The performance of *gracilis* in the shock situation did not appear to be affected by experience; the longitudinal and the cross-sectional groups

in both the first and last trials were approximately of the same magnitude. In contrast, the longitudinal *bairdii* group spent more time on the pan with an increase in age.. Both age and experience contributed to the performance of the longitudinal *bairdii* group as indicated by a comparison of its performance with the first trials of the cross-sectional groups. The importance of experience is revealed by the cross-sectional groups, whose duration on the pan increased from one trial to the next after 15 days of age (Fig. 6). *Bairdii's* experiences in the situation apparently reinforced its genotypic divergence from *gracilis*.

The 70 day shock test demonstrated no consistent effect of the early experience on the later performance of the various age groups. This finding agrees, in general, with that of Denenberg (1958) who used inbred house mice in a classical conditioning situation. Both *bairdii* and *gracilis* spent significantly more time on the pan during the last trial than during the first trial. The change in performance of *bairdii* was significantly greater than that of *gracilis* (Table IV). Similar experiences apparently have a differential effect on the behaviour of the two subspecies.

Differences in the types and frequency of responses given by each subspecies during their development apparently provide the basis for differential reinforcement from environmental stimuli. The tendency of the mice to sit on the pan in the shock situation was reinforced more often and to a greater extent in *bairdii* than in *gracilis*. The probability of the sitting response increased in *bairdii*, while the less suitable responses of *gracilis*, such as jumping, may have been reinforced and interfered with the development of the sitting response. In another learning situation, which required the mice to press a small treadle to avoid shock (King, 1959), the characteristic jumping response of *gracilis* tended to be reinforced, because the probability of hitting the treadle was increased by their jumping. Environmental stimuli may then channel the development of maturing behavioural patterns in the direction most suitable for adaptation to a particular habitat. In nature, the innate responses of *bairdii* may be reinforced more in its native grassland habitat than in other types of habitat, while the forest habitat of *gracilis* would reinforce the development of its innate responses. Ecologic separation of these two subspecies could then depend upon the probability with which the environment reinforces the early behaviour of each subspecies. That habitat providing each subspecies with the most reinforcement would be selected. Thus, a mouse may select the habitat in which it has the maximum opportunity to learn.

Summary

The development of behaviour in *Peromyscus maniculatus bairdii* and *P. m. gracilis* was studied in two types of aversive situations. Longitudinal and cross-sectional groups of both subspecies, totalling 320 mice, were tested for the ability to escape from water and from an electrified grid.

Between 16 and 22 days of age, *P. m. gracilis* was slower to escape from water than *bairdii*, but later performed like *bairdii*. This difference in swimming performance was attributed to differences in the rate of physical maturation of the two subspecies.

The tendency to remain on top of a platform above the water was more characteristic of *bairdii* than of *gracilis*, although both subspecies increased their duration on the platform with experience in the situation.

P. m. bairdii escaped from an electric shock for longer periods than *gracilis*. The performance of *bairdii* improved with accumulated experiences in this situation, while the performance of *gracilis* did not change appreciably.

Three factors were postulated as explanations for the differences in performances of the two subspecies: rate of physical maturation, genetic determinants of behaviour, and effect of experience. Each of these factors interacts with the others to produce the adult behaviour of the mice.

REFERENCES

Barbahenn, K. R. & New, J. G. (1957). Possible natural intergradation between prairie and forest deermice. *J. Mamm.*, **38**, 210-218.

Denenberg, V. H. (1958). Effects of age and early experience upon conditioning in the C57BL/10 mouse. *J. Psychol.*, **46**, 211-226.

Foster, D. D. (1959). Differences in behaviour and temperament between two races of the deer mouse. *J. Mamm.*, **40**, 496-513.

Hall, E. R. & Kelson, K. R. (1959). *The Mammals of North America*. New York: Ronald Press.

Harris, V. T. (1952). An experimental study of habitat selection by the prairie and forest races of the deermouse, *Peromyscus maniculatus*. *Contr. Lab. Vert. Biol.*, Univ. Mich., **56**, 1-53.

Hooper, E. T. (1942). An effect on the *Peromyscus maniculatus* Rassenkries of land utilization in Michigan. *J. Mamm.*, **23**, 193-196.

King, J. A. (1958). Maternal behaviour and behavioural development in two subspecies of *Peromyscus maniculatus*. *J. Mamm.*, **39**, 177-190.

Lindquist, E. F. (1953). *Design and Analysis of Experiments in Psychology and Education*. Boston: Houghton Mifflin Co.

McIntosh, W. B. (1955). The applicability of covariance analysis for comparison of body and skeletal measurements between two races of the deer-mouse, *Peromyscus maniculatus*. *Contr. Lab. Vert. Biol.*, Univ. Mich., **72**, 1-54.

Svihla, A. (1932). A comparative life history study of the mice of the genus *Peromyscus*. *Misc. Publ., Mus. Zool.*, Univ. Mich., **24**, 1-39.

Svihla, A. (1935). Development and growth of the prairie deermouse, *Peromyscus maniculatus bairdii*. *J. Mamm.*, **16**, 109-115.

Accepted for publication 24*th February*, 1961.

THE RELATIONSHIP OF SOCIAL COMPETITION WITH ENDOCRINE WEIGHTS AND ACTIVITY IN MALE CHICKENS

By H. S. SIEGEL and P. B. SIEGEL

Poultry Department, Virginia Polytechnic Institute, Blacksburg

Since the original observations of Schjelderup-Ebbe (1913) dominance or peck orders in flocks of chickens have been studied by several workers. Guhl (1953), reviewing the subject, indicated that higher ranking birds have precedence at feeders and roosts, possess greater freedom of the pen and, in the case of males, greater freedom to mate. In contrast, lowest ranking individuals might become harassed to the point of starvation. Guhl & Allee (1944) concluded that socially well integrated flocks pecked less and were generally more productive than those where social tensions were high. These conclusions have been further substantiated by Tindell & Craig (1959).

It seems possible, therefore, that birds low in the dominance order or in flocks where increased social tensions exist may be subjected to sufficient stimuli to produce some evidences of physiological stress. Briefly, this may be described as stimulation of the pituitary-adrenal axis, with a resultant increase in adrenal weight and function and concomitant changes in the target organs of adrenal secretions (Selye, 1950). Evidence of a relationship between the degree of social tension and adrenal weights has been reported by Christian (1955) who found that mice maintained in groups had significantly heavier adrenals than those kept in isolation. It has also been reported that adrenals of subordinate rats (Barnett, 1955) and mice (Davis & Christian, 1957) are of greater size than those of more dominant individuals. Vanderbergh (1960) using relative degree of eosinopenia as a quantitative measure of severity of stress in albino rats, observed significant declines in eosinophil counts in grouped mice as compared to isolated individuals. He also noted that the subordinate mice showed more severe eosinopenia than did the dominant individuals.

Little work along these lines has been reported for the avian species. Since chickens react physiologically to stressing stimuli in a manner similar to mammals (Garren & Shaffner, 1956), it was of interest to study conditions in which social competition might influence the weight and function of endocrine glands in male chickens. This study was accomplished in a series of 4 experiments as follows:

Experiment	Relationships studied	No. of Birds
1	Relative aggressiveness to endocrine weight	28
2	Social rank to endocrine weight	12
3	Effect of introducing individuals into strange flocks on endocrine weights and function	32
4	Influence of continuous isolation, alternate isolation and grouping, and continuous grouping on endocrine weights and function	30

Methods and Results

Experiment 1

To determine whether degree of aggressiveness is in itself related to endocrine weight, 28 White Plymouth Rock males, 370 days of age, were selected from a group in which the relative aggressiveness of the individuals had been previously determined as a result of 8 randomly paired initial encounters (P. B. Siegel, 1960). The percentage of encounters won by the selected birds ranged from 0 to 100.

Males were sacrificed by severing the external jugular; adrenals, thyroids and pituitaries were removed and weighed to the nearest 0·1 mg.; and testes and spleens were weighed to the nearest 1·0 mg. After adjustment to mg. per 100 g. of body weight, the gland weights were phenotypically correlated with the arc sin transformations of the percentage of initial paired encounters won according to methods described by Snedecor (1946). The mean gland and organ weights as mg. per 100 g. body weight and their correlation coefficients (r) with relative aggressiveness are shown in Table I. All relationships were of low order and not significant.

Experiment 2

Although relative aggressiveness in itself was not significantly correlated with gland weights, it

Table I. Endocrine Gland and Organ Weights and Their Correlations with Relative Aggressiveness for 28 Adult WPR Males.

Gland or organ	Means ± S.D.	Correlation with relative aggressiveness
	Mg/100g. body wt.	r*
Adrenal	6·87 ± 1·35	—·005
Thyroid	6·69 ± 2·21	·158
Pituitary	0·37 ± 0·10	—·025
Testes	698·8 ± 240·0	·041
Spleen	133·2 ± 30·0	·201

*Significance of r at $P<0·05 = ·374$

seemed possible that birds subordinate in the social hierarchy might be subjected to sufficient stimulation to induce changes in the pituitary-adrenal axis. This could be true especially during the formative stages of the peck order. Thus, two 6-bird groups of White Plymouth Rock males, 390 days of age, were placed in separate 4′ × 8′ pens. The groups were designated as A and B. By observation, it was determined that Group A did not establish a stable peck order until 5 days after the males were placed in the pen, while in Group B no changes occurred after the first day. Six days following formation of the groups, all birds were sacrificed and the weights of adrenals, thyroids, pituitary, spleen and testes were obtained as in Experiment 1. The gland weights of individual birds as mg. per 100 g. of body weight were correlated with the number of birds dominated by that individual. These data are shown in Table II.

Correlations of gland weights with social rank were not significant. Of note, however, was the lack of consistency between groups in the sign and magnitude of the relationships of adrenal and testes weight with social rank. The negative correlation coefficient of ·760 for adrenal weight in Group B approaches significance at the 5 per cent. level of probability, while the positive value of ·368 in Group A is of lower order. The relationship of testes weight with social rank in group B is positive and approaches significance, but in Group A it is negative and quite low. The differences between groups for gland and organ weights were not significant.

Experiment 3

This experiment was initiated to determine whether placing male chickens into pens with strange males for short periods of time would affect their endocrine glands. White Leghorn males, which were 105 days of age, were randomized into 4 groups of 8 birds each. These groups, designated A, B, C, and D, were maintained in 4′ × 8′ pens with muslin curtains hung on the separating wire partitions to prevent visual contact between flocks. The groups were observed daily for 3 days and peck orders noted. Birds from Groups C and D, designated as experimentals, were then introduced singly, into one of 4 pens containing 50 strange males for a 4-hour period each day. A rotation procedure was established so that each male in Groups C

Table II. Endocrine Gland and Organ Weights and their Correlations with Social Rank in Two Groups of 6 Adult WPR Males

Gland or organ	Group A		Group B	
	Mean ± S.D.	Correlation with social rank*	Means ± S.D.	Correlation with social rank*
	Mg/100g. body wt.	r†	Mg/100g. body wt.	r†
Adrenal	7·43 ± 1·64	·368	6·19 ± 1·43	—·760
Thyroid	6·17 ± 1·49	—·178	5·69 ± 2·18	·333
Pituitary	0·51 ± 0·25	·070	0·47 ± 0·10	·302
Testes	850·3 ± 240·0	—·117	701·8 ± 240·0	·804
Spleen	153·0 ± 40·0	—·110	193·4 ± 80·0	—·188

*Social rank—number of birds in the group dominated by an individual male.
†Significance of r at $P<0·05=·811$

and D was placed in the same pen a maximum of 6 times during the 22-day experimental period. Groups A and B were maintained as controls and had no visual contact with birds other than those in their own flock during the experiment. Because it was possible that handling and carrying the experimental birds to and from the strange pens might in themselves be stimuli, the control flocks were also handled and carried about their respective pens each time the experimental birds were moved.

The body weight of each male was obtained when the groups were formed and just prior to sacrifice on the 23rd day. Adrenals, thyroids, anterior pituitaries, spleens and testes were removed and weighed as previously described except that the right and left adrenals were weighed separately. It has been observed that the left adrenal of chickens may be more sensitive to an environmental stressing agent than the right (H. S. Siegel, 1960).

Since cholesterol is considered a precurser of adrenal steroids (Rosenfeld, 1955), depletion of cholesterol may indicate hyperactivity of the gland. Thus, adrenal glands were marked for identification and stored at —20°C. for future total cholesterol determinations according to the method described by Knobil *et al.* (1954).

Several investigators have reported cholesteraemia following emotional or mental stress in man (Westlake, *et al.* 1958), rats (Selye, 1950) and chickens (Wiley, *et al.*, 1957). It seemed possible therefore, that placing birds with strangers might induce a rise in plasma cholesterol levels. Thus, just prior to sacrifice, a blood sample was obtained from each bird by cardiac puncture. These samples were then centrifuged and the plasma stored at —20°C. for future total cholesterol determinations according to the Zlatkis, *et al.* (1953) method.

Differences in gland weights as mg. per 100 g. of body weight, adrenal cholesterol as μg. per mg. of adrenal, and plasma cholesterol in mg. per cent., between control and experimental groups were subjected to analysis of variance. Correlation coefficients were computed for the various gland and organ weights and cholesterol concentrations with social rank in each duplicate group. The within group correlations were then tested for homogeneity.

Shown in Table III are mean gland and organ weights and cholesterol concentrations for the control and experimental groups. It will be noted that the left adrenals of those birds which were placed in strange pens for 4 hours per day were significantly heavier than those of the controls

Table III. Effect of Placing W.L. Cockerels in Pens Containing 50 Strange Males on Endocrine Gland and Organ Weights and Adrenal and Plasma Cholesterol Concentrations.†

	Means±S.D.		
	Experimentals (E)	Controls (C)	Difference (E-C)
22 day gain in body weight, g.	158·3±119·6	239·3 ±126·7	—81·0
Right adrenal, mg/100g. body weight	6·04± 0·87	5·97± 1·32	0·07
Left adrenal, mg/100g. body weight	5·46± 0·64	4·87± 0·76	0·59*
Both adrenals, mg/100g. body weight	11·50± 1·43	10·84± 1·88	0·66
Thyroid, mg/100g. body weight	5·31± 1·60	5·47± 1·40	—0·16
Anterior pituitary, mg/100g. body weight	0·34± 0·12	0·31± 0·12	—0·03
Spleen, mg/100g. body weight	157·1 ± 49·6	167·7 ± 35·8	—10·6
Testes, mg/100g. body weight	380·7 ±160·1	326·8 ±268·6	53·9
Adrenal cholesterol, μg./mg. adrenal	39·61± 5·71	37·96± 6·94	1·65
Plasma total cholesterol, mg. %	128·93± 19·50	147·64± 15·40	—18·71*

†At 15 weeks of age each cockerel in the experimental group spent 4 hours daily, for 22 consecutive days, in a pen containing 50 males with whom he was unacquainted.

*$P<0·05$.

($P<0{\cdot}05$). Furthermore, contrary to expectations, plasma cholesterol levels in the experimental groups were significantly lower than those of the controls. The differences between groups for other gland weights, 22 day gain in body weight, and adrenal cholesterol concentrations were not significant.

It was possible to calculate average correlation coefficients for social rank with the various physiological factors because the correlations within groups were homogeneous. These are listed in Table IV. A significant negative average correlation coefficient of ·692 for left adrenal weight with social rank was calculated in the control flock, but this relationship was not significant in the experimentals. This does not necessarily contradict the results obtained in Experiment 1 because the measurements of aggressiveness differed. The relationships of other gland weights, cholesterol levels and body weight gains with position in the peck order were found to be low.

Table IV. Relationships of Social Rank Within Groups with Endocrine Gland and Organ Weights and Adrenal and Plasma Cholesterol Levels in W.L. Males 127 days of age which were Rotated Daily into Pens with 50 Strange Males.

	Average correlation coefficients with social rank*	
	Experimentals	Controls
22 day gain in bodyweight	—·482	·479
Left adrenal	—·187	—·692*
Right adrenal	—·163	—·243
Both adrenals	—·160	—·619
Thyroid	·478	·169
Anterior pituitary	—·140	·008
Spleen	—·222	—·259
Testes	—·186	—·013
Adrenal cholesterol	—·215	—·274
Plasma cholesterol	·358	·151

*Number of birds dominated by individual.
*$P<0{\cdot}05$

Experiment 4

In the three previous experiments comparisons were made between chickens maintained in flocks or groups. Consideration was next given to the influence that continuous isolation, alternate isolation and grouping, and continuous grouping might have on endocrine weights and cholesterol levels of the adrenals and plasma.

Athens-Canadian Randombred males, 266 days of age were randomly divided into 3 treatment groups. These were replicated so that each replicate or sub-group was made up of 5 males, making a total of 10 birds per treatment. Prior to the start of the experimental period all birds had been maintained in individual cages for a period of 207 days. The cages, constructed with solid partitions between birds, prevented physical contact. However, visual contact, although limited to sight through the front of the cage, and audio contact were not prevented.

The following social conditions were compared for their effects on endocrine activity: (1) *Individually caged*—These males remained in the cages throughout the 21 day experimental period. (2) *Alternately caged and grouped*—Each 5-bird sub-group was placed in a $4' \times 8'$ pen for a period of 4 hours daily (8 a.m. to 12 noon). During the remainder of the day they were maintained in the individual cages. (3) *Continuously grouped*—The two 5-bird groups were confined to $4' \times 8'$ pens for the entire 21-day period.

Peck order rankings were recorded in those groups which were continuously together and in those grouped 4 hours per day. At the termination of the experimental period, the males were sacrificed and endocrine weights and adrenal and plasma total cholesterol concentrations determined as previously described. Differences among treatment groups were examined by analysis of variance and a modification of Duncan's (1955) Multiple Range Test (Kramer, 1956). Within replicate correlation coefficients were calculated for the relationships of social rank with the various endocrine data and these were tested for homogeneity within treatment groups.

Shown in Table V are the mean gland and organ weights and cholesterol values obtained in Experiment 4. Since none of the replicate differences were significant, replicates were pooled and overall treatment means shown. It will be noted that both the left and right adrenals of the birds grouped continuously were significantly heavier than those kept in individual cages ($P<0{\cdot}01$). Adrenals of the males grouped 4 hours daily were intermediate to the others. Differences for other gland and organ weights

Table V. Mean and Standard Deviations of Endocrine Gland and Organ Weights and Adrenal and Plasma Cholesterol Levels of Adult Athens--Canadian Randombred Males Maintained in Individual Cages, in Groups 4 hours and Caged for 20 hours per Day, and in Groups Continuously.

	Individual cages	Grouped	
		4 hrs./day	Continuously
Number of birds sacrificed	9	10	10
Right adrenal, mg/100g. body weight	2·54± 0·74[a]	3·41± 0·53[a b]	3·64± 0·37[b]
Left adrenal, mg/100g. ody weight	2·58± 0·71[a]	3·30± 0·75[a b]	3·87± 0·74[b]
Thyroid, mg/100g. body weight	6·10± 1·58[a]	5·02± 1·28[a]	5·56± 1·68[a]
Anterior pituitary, mg/100g. body weight	0·32± 0·07[a]	0·29± 0·06[a]	0·29± 0·07[a]
Testes, mg/100g. body weight	810·0 ±270·0[a]	970·0 ±280·0[a]	850·0 ±170·0[a]
Spleen, mg/100g. body weight	108·7 ± 26·3[a]	110·0 ± 30·6[a]	113·8 ± 26·7[a]
Adrenal cholesterol, μg./mg. adrenal	27·74± 7·40[a]	27·37± 5·10[a]	25·59± 4·32[a]
Plasma cholesterol, mg. %	120·78± 48·20[a]	140·20± 24·42[a]	138·80± 46·14[a]

Treatment means whose superscripts differ are significantly different ($P<0·01$).

and the total cholesterol concentrations of the adrenals and plasma were not significant.

The relationships of social rank within treatments with endocrine gland and organ weights and total cholesterol levels for birds grouped 4 hours per day and those grouped continuously are shown in Table VI. A significant negative correlation coefficient was calculated for left adrenal weight with social rank in the flocks grouped for 4 hours per day, indicating that the lower the social rank the greater the adrenal weight. Although the right adrenal and pituitary relationships were also negative and quite high, these were not statistically significant.

In contrast to the relationships observed in the alternately grouped flocks, were those found in flocks grouped continuously. Not only were correlation coefficients of noticeably lower magnitude, but they were also of opposite sign.

Table VI. Relationships of Social Rank Within Treatments with Endocrine Gland and Organ Weight and Adrenal and Plasma Cholesterol Levels in Adult Athens-Canadian Randombred Males Grouped for 4 hours per day and in Groups Continuously.

	Average correlation co-efficients with social rank†	
	Grouped 4 hrs per day	Grouped continuously
Left adrenal	—·843*	·429
Right adrenal	—·785	·361
Thyroid	·082	·383
Anterior pituitary	—·755	·695
Testes	·168	·213
Spleen	·595	—·094
Adrenal cholesterol	·010	·319
Plasma cholesterol	·417	·269

†Number of birds dominated by an individual.
*$P<0·05$

Discussion

If physiological stress is present in chickens low in the dominance order or in flocks where high levels of social tension exist, one should expect certain evidences of hyperstimulation of the pituitary-adrenal axis. Adrenal weights relative to body weight should increase concomitant to declines in spleen weights. This was observed by Garren & Shaffner (1956) in New Hampshire chickens subjected to purely physical stressors. However, as observed in Experiment 1, degree of aggressiveness was not related to either adrenal or spleen weight in male chickens. Therefore, if differential adrenal patterns do arise within social groups they might be interpreted as an effect rather than a cause of social rank.

Social tensions are high during the formative stages of the peck order (Guhl, 1953), with the greatest number of encounters between birds occurring during this period (Marks, *et al.*,1960). In Experiment 2, however, no significant relationships between rank status and gland weights were observed when birds were autopsied shortly after the males were placed together in flocks. The noticeable lack of consistency between A and B in sign and magnitude of the correlation coefficients of adrenal and testes weights with social rank deserves some comment. In Group A, where the relationships of testes and adrenal weights with social ranking were low, 5 days were required for the stable establishment of a peck order. In contrast, when rapid formation of a peck order was accomplished (Group B), these correlation coefficients approached significance. It seems possible that in unstable populations, both high and low ranking individuals may be subjected to stressing stimuli.

When a small number of strange hens is introduced into a socially established flock, egg production of this minority group may temporarily decline or cease (Sanctuary, 1932). Typically, a newcomer enters as the lowest ranking individual in the flock (Guhl & Allee, 1944). Observations, in Experiment 3, of males introduced singly into pens of 50 strange males concur with these reports. The stranger was immediately attacked, and in all but a few cases, the newcomer avoided the attackers and attempted to hide under feed hoppers or in corners. This was sufficient to induce significant hypertrophy of the left adrenal. These results are in agreement with those obtained by Clarke (1953), who found that the adrenal weights of voles were increased concomitant to a decrease in thymus weight after these animals had been introduced into cages with aggressive strangers. Neither right adrenal nor spleen weights were significantly changed however. When the relationships between social rank and gland weights were determined, a significant negative correlation coefficient with left adrenal weight was obtained only in the groups not placed in flocks of strange males.

To clarify further the role played by social competition in adrenal weight responses, comparisons, in Experiment 4, were made among groups of males which were individually caged, together for 4 hours per day, and together continuously. Both right and left adrenals relative to body weight were significantly ($P<0{\cdot}01$) heavier in birds maintained together continuously than in those kept in cages. Right and left adrenals for the males grouped together for 4 hours per day were intermediate in weight to the others. These results are in agreement with those reported for grouped and isolated mice by Christian (1959). Christian (1959) also found splenic hypertrophy and diminished weights of reproductive organs in grouped mice, however, no significant changes in spleen or testes weights as a result of social competition were found in these male chickens. When position in social rank was correlated with gland weights in Experiment 4, only the relationship involving the left adrenal weights of the birds grouped for 4 hours per day was significant.

The levels of total plasma cholesterol reported herein are within the ranges reported by other investigators for male chickens of this age (Lorenz, *et al.*, 1938; Weiss, 1957). The significanly lower concentrations in the plasma of birds introduced daily into pens with strangers may appear to be at variance with reports that emotional or mental stress induces hypercholesteraemia in man (Westlake, *et al.*, 1958). The results obtained by Kuhl, *et al.* (1955), however, indicate that such a rise in blood cholesterol may be only transient. If this is true, it seems probable that the hypercholesteraemia may have disappeared during the 22 day experimental period. It is also possible that an increased lipid catabolism necessary to satisfy energy needs, coupled with reduced feed intake might account for this decline in the Experimental groups reported herein. Depressed weight gains in these groups, although not significant, support this suggestion.

The weights of thyroid, pituitary, testes and spleen were not significantly affected by any of the conditions imposed on the birds in these experiments. In spite of significant increases in the weights of adrenal glands, the concentration of total cholesterol in the adrenal was not depressed. According to Selye (1950) cholesterol depletion is typical during the alarm phases of adaptation, but levels reach or surpass normal during the resistance phase. Peck order ranking could not be correlated to gland weights, other than the left adrenal; nor could it be related to cholesterol levels, indicating that under these experimental conditions social rank did not significantly affect the entire endocrine system.

The results of these experiments with male chickens agree essentially with those of Davis & Christian (1957), who in investigations with mice observed that lower ranking individuals

had heavier adrenals than higher ranking ones. They concluded that this difference was the result of greater physical and psychological stimulation. It should be noted that in the present experiments, only left adrenal weights were significantly correlated to position in social rank, which supports the suggestion that the left gland of fowl is relatively more sensitive to environmental variation than is the right (H. S. Siegel, 1960; Siegel & Siegel, 1960). The relationship of ranking to adrenal weight appears to be overshadowed by a relatively greater behavioural disturbance which may be distributed over the entire group. Thus when the adrenal weights of the group as a whole were increased as a result of increased social tensions—(Experiments 3 and 4) significant expression of the relationships of social rank with adrenal activity were not apparent. It is also possible that the avian species are less liabile to psychological or "emotional" stimulation than mammals.

Summary

Four experiments were conducted to study conditions in which social competition might influence the weight and function of endocrine glands. The results indicated that:

(1) Aggressiveness *per se* was not phenotypically related to endocrine weight.

(2) The left adrenals of male chickens placed as a minority in pens of strangers were significantly heavier than those of birds remaining in their own flocks. Plasma cholesterol levels of these males were also depressed.

(3) There was a highly significant increase in the weights of both left and right adrenals in males maintained in groups continuously as compared to those kept in individual cages.

(4) The relationship between social rank and left adrenal weight was significant only when other types of social competition were minimized.

(5) Weights of thyroid, pituitary, spleen and testes and levels of cholesterol in the adrenals were not significantly affected by the social conditions imposed in these experiments.

Acknowledgments

The authors wish to thank Dr. A. M. Guhl, Kansas State College, Dr. E. B. Hale, Pennsylvania State University, and Dr. C. E. Howes, Virginia Polytechnic Institute for reading the manuscript and offering constructive criticisms and suggestions.

REFERENCES

Barnett, S. A. (1955). Competition among wild rats. *Nature*, **175,** 126-127.

Christian, J. J. (1955). Effect of population size on the adrenal glands and reproductive organs of male mice in populations of fixed size. *Amer. J. Physiol.*, **182,** 292-300.

Christian, J. J. (1959). Adrenocortical, splenic and reproductive responses of mice to inanition and grouping. *Endocrinology*, **65,** 189-197.

Clarke, J. R. (1953). The effect of fighting on the adrenals, thymus and spleen of the vole (*microtus Agrestis*). *J. Endocr.*, **9,** 114-126.

Davis, D. E. & Christian J. J. (1957). Relation of adrenal weight to social rank of mice. *Proc. Soc. Exp. Biol. Med.*, **94,** 728-731.

Duncan, D. B. (1955). Multiple range and multiple F. tests. *Biometrics*, **11,** 1-42.

Garren, H. W. & Shaffner, C. S. (1956). How the period of different stress stimuli affects the endocrine and lymphatic gland weights of young chickens. *Poult. Sci.*, **34,** 266-272.

Guhl, A. M. (1953). Social behaviour of the domestic fowl. *Kansas Agr. Exp. Sta. Tech. Bull.*, **73,** 1-48.

Guhl, A. M. & Allee, W. C. (1944). Some measureable effects of social organization in flocks of hens. *Physiol. Zool.*, **17,** 320-347.

Knobil, E., Hagney, M. C., Wilder, E. I. & Briggs, F. N. (1954). Simplified method for determination of total adrenal cholesterol. *Proc. Soc. Exp. Biol. Med.*, **87,** 48-50.

Kramer, C. Y. (1956). Extension of multiple range tests to group means with unequal numbers of replications. *Biometrics*, **12,** 307-310.

Kuhl, W. J., Beck E. M., Gershberg, E. H., Street, E. & Rolli, E. P. (1955). Effect of cold water stress on blood and urine constituents in 55 normal male subjects. *Metabolism*, **4,** 143-152.

Lorenz, F. W., Enterman, C. & Chaikoff, I. L. (1938). The influence of age, sex and ovarian activity on blood lipids of the domestic fowl. *J. Biol. Chem.*, **122,** 619-633.

Marks, H. L., Siegel, P. B. & Kramer, C. Y. (1960). Effects of comb and wattle removal on the social organization of mixed flocks of chickens. *An. Behav.*, **8,** 192-196.

Rosenfeld, G. (1955). Steroidogenisis by intact calf adrenals perfused *in vitro*. *Endocrinology*, **56,** 649-666.

Santuary, W. C. (1932). A study of avain behaviour to determine the nature and peristancy of the order of dominance in the domestic fowl and to relate these to certain physiological reactions. *M.S. Thesis*, Massachusetts State College, Amherst.

Schjelderup-Ebbe, T. (1913). Honsenes stemme. Bidrag til honsenes psyhologi. *Naturen*, **37,** 262-276.

Selye, H. (1950). *The physiology and pathology of exposure to stress*. Aeta Inc., Montreal, Canada.

Siegel, H. S. (1960). Effect of population density on the pituitary-adrenal cortical axis of cockerels. *Poult. Sci.*, **39,** 500-510.

Siegel, P. B. (1960). A method of evaluating aggressiveness in chickens. *Poult. Sci.*, **39,** 1046-1048.

Siegel, P. B. & Siegel, H. S. (1960). Genetic parameters of gland and body weights. *Jour. Hered.*, **51,** 59-62.

Snedecor, G. W. (1946). *Statistical methods*. Ames, Iowa: Iowa State College Press.

Tindell, D. & Craig, J. V. (1959). Effects of social competition on laying house performance in the chicken. *Poult. Sci.*, **38**, 95-105.

Vandenbergh, J. G. (1960). Eosinophil response to aggressive behaviour in CFW albino mice. *Anim. Behav.*, **8**, 13-18.

Weiss, H. S. (1957). Age related changes in plasma cholesterol of chickens. *Proc. Soc. exp. Biol. Med.*, **95**, 487-489.

Westlake, P. T., Wilcox, A. A., Haley, M. I. & Peterson, J. E. (1958). Relationship of mental and emotional stress to serum cholesterol levels. *Proc. Soc. exp. Biol. Med.*, **97**, 164-165.

Wiley, H., Freidman, M. & Agello, C. (1957). Atherosclerotic response of "agressive" and "passive" groups of chickens to a cholesterol enriched diet. *Proc. Soc. exp. Biol. Med.*, **96**, 244-246.

Zlakis, A., Zak, B. & Boyle, A. (1953). A new method for direct determination of serum cholesterol. *J. lab. clin. Med.*, **41**, 486-492.

Accepted for publication 31*st December*, 1960.

PROPERTIES OF THE VISUAL STIMULI FOR THE APPROACH RESPONSE IN THE DOMESTIC CHICK

By F. V. SMITH and P. A. HOYES
Department of Psychology, University of Durham, England

As previously reported by Smith (1960) many chicks of the domestic fowl (Light Sussex x Brown Leghorn) will approach and remain before a number of intermittent stimuli operating at one position in space. During approach and in the vicinity of the stimulus loud 'fear' chirps were replaced by soft 'contentment' chirps and by a lowering of the head and pecking. The stimuli included a black sector (45°) painted on a 12 inch white disc rotated at one revolution per 1·5 seconds and a circular patch of light, 6 inches in diameter which was 'on' for 1/4 second and 'off' for 3/4 second. The stimuli were presented at one position in space and individuals of different groups of chicks from identical batches moved towards them in proportions which were not significantly different. The rotating sector was, however, approached significantly more often than the same disc and sector attached to a cylinder and moved towards and away from the chicks, without being rotated. James (1959, 1960) in papers received since these experiments were undertaken, has used flicker rates from ·25 to 5 second on/off as unconditioned stimuli for 'imprinting' on nearby objects. Several studies, including those of Fabricius (1951), Ramsay & Hess (1954), Hinde, Thorpe & Vince (1956), and Lorenz (1957) have reported that birds of different species will approach and follow a variety of objects moving away from them; but the above results suggested that the properties of the visual stimuli capable of inducing initial approach could be explored further. One issue arising from the results with the rotating sector, for example, was the relative effectiveness of the horizontal and vertical components in an intermittent stimulus operating at one position in space.

General Method

Chicks of the domestic fowl (Light Sussex x Brown Leghorn) were used. Unless otherwise stated, they were tested within 18 to 30 hours after hatching in an incubator. After hatching and between trials, they were kept in darkened boxes in heated cupboards but were not isolated. In all experiments (except Experiment 10) they were placed facing at right angles to the direction of approach to the stimulus. No external reinforcement such as food, water or access to greater warmth was associated with the stimuli.

Experiment 1. Vertical Compared with Horizontal Oscillation

Method

Parallel lines 1 inch wide and 1½ inches apart were painted in Indian ink on a sheet of white Bristol Board 24 inches × 16 inches. This was arranged so that the lines could be presented as oscillating vertically or horizontally behind an aperture 6 inches × 6 inches in the end of a run 4 feet 6 inches × 3 feet with lower edge 3 inches from the table surface on which the chick moved. The effect visible to the chick was 4 lines moving up in a second and 4 lines moving down in a second, across the aperture. The same timing was used for the to and fro, horizontal movement. The apparatus was silent in operation. The chicks were placed 3 feet 6 inches from the pattern of lines. Each chick was in the enclosure 10 minutes and was judged to have approached the stimulus if it came within 6 inches and remained in the vicinity. Approximately 25 minutes later, the chick was presented with the alternative stimulus, so that both stimuli, oscillating vertical and horizontal lines, were each exposed to 30 chicks, 15 as a first presentation and 15 as a second presentation. Group 1 contained 8 females and Group 2, 7.

Results

(i) The number approaching the stimulus at each presentation is given in Table I.

A slight advantage in favour of the vertical oscillation is indicated; but the difference is not significant at ·05 level either at first or second presentation in terms of Fisher's Exact Probability Test (Finney, 1948, adaptation; see also Siegel, 1956). No significant differences were found between the times of first movement to the two stimuli.

Table I.

Stimulus	Approach at first presentation		Approach at second presentation	
	Yes	No	Yes	No
Vertical oscillation	12 (6M.6F.)	3	9 (5M.4F.)	6
Horizontal oscillation	10 (6M.4F.)	5	12 (6M.6F.)	3

Experiment 2. The Relationship between Effectiveness and Size of the Stimulus

Method and Materials

As previously reported by Smith (1960), a disc of light, 6 inches in diameter (15·3 amp) alternatively 'on' and 'off' is an effective stimulus in inducing the approach response. The present experiment was designed to explore the possibility that variations in diameter of the disc might be associated with effectiveness. The variations in diameter of the stimulus were secured by cutting a circular hole in a black box containing a lamp bulb and inserting masks with holes of different diameters between a sheet of frosted glass on the inside and a cover of black carbon paper on the outside of the box. With a 6 inch disc a barrier layer cell applied to the outer surface recorded a light intensity of ·5 foot candles at the centre. A timing apparatus, set up in a distant basement to avoid noise, gave an on/off ratio of ½ second. To human observation, the effect at all diameters was the 'Gamma' phenomenon, of expansion until the total disc was illuminated and then disappearance, with apparent contraction (Koffka, 1935). In effect this arrangement gave an apparent movement, equally in all directions from the centre.

The chick was placed half way along the floor of a run 10 feet × 2 feet 6 inches × 2 feet high. Each chick was exposed to the stimulus for 5 minutes, 24 chicks from 4 batches being involved. The four diameters were presented in a different order for each chick so that all the permutations of order of presentation of the four were achieved.

Results

The number of approaches to the various diameters in the different orders of presentation is set out in Table II.

A total of 100 presentations, each of five minutes duration, was made.

The implication that larger diameters might be more effective was tested further.

Experiment 3. Comparison of Effectiveness as Stimuli of Diameters 1 cm. and 15·3 cm.

Method

The two diameters were presented in the same conditions as for Experiment 2 to individual chicks of two independent groups of 8, 6 in each group from one batch and 2 from another. Approximately 25 minutes later, the chicks were exposed to the other stimulus. Each group contained an equal number of each sex.

Results

The number of each group responding to each stimulus is shown in Table III.

Table II.

Stimulus	Order of Presentation				Total No. of
	1st	2nd	3rd	4th	Approaches
Diam. 1 cm.	0	0	1	1	2 (1M. 1F.)
4·5 cm.	0	2	4	2	8 (6M. 2F.)
9 cm.	1	3	2	5	11 (5M. 6F.)
15·3 cm.	3	1	1	4	9 (3M. 6F.)
Totals	4	6	8	12	30

Table III

Stimulus	1st presentation		2nd presentation	
	Yes	No	Yes	No
Diam. 1 cm.	0	8	0	8
Diam. 15·3 cm.	6 (3F.3M.)	2	4 (4M)	4
	P = ·00349 under null hypothesis.		P = ·0384 under null hypothesis	

The difference between the number of approaches to the two diameters at first presentation is significant at the ·005 level in terms of Fisher's Exact Probability Test (Finney, 1948 adaptation) and the difference at second presentation at the ·05 level.

Experiment 4

This experiment was designed to indicate the relative effectiveness of intermittent stimuli of different diameters, the choice of which was influenced by the results from Experiments 2 and 3 and a number of preliminary trials.

Method

The experimental conditions were as for Experiments 2 and 3, except that a brighter light was used. The chick was exposed to the stimulus for 7 minutes and was judged to have approached if it consistently moved towards the stimulus and covered more than two-thirds of the total distance of 4 feet. The diameters chosen were 7 cm., 10 cm., 15·3 cm., and 28 cm. The position of the lamp behind the frosted glass was adjusted to secure approximately uniform illumination over the disc, though naturally there was some decline from the centre to the periphery. A barrier layer cell applied to the outside of the discs gave readings at the centre which varied between 1·2 and 1·0 foot candles and between ·8 and ·6 foot candles at the periphery, for all four discs. These readings were taken while the light was continuously 'on' for some time and from the front of the disc. In view of the experience within the department of considerable variability between batches, chicks were allotted in equal numbers to each diameter from each batch; 100 chicks from 8 batches were involved, i.e. 25 to each diameter.

Results

(i) Initial responses to intermittent stimuli of the four diameters are shown in Table IV.

Applications of χ^2 test to the differences gives:

(*a*) between no. of responses at 7 cm. and at 15·3 cm. $\chi^2=9{\cdot}5$, df.$=1$, $\cdot 01>P>\cdot 001$.

(*b*) between no. of responses at 7 cm. and at 28 cm., $\chi^2=8{\cdot}03$, df.$=1$, $\cdot 01>P>\cdot 001$.

(*c*) between no. of responses at 10 cm. and at 15·3 cm., $\chi^2=4{\cdot}25$, df.$=1$, $\cdot 05>P>\cdot 02$.

(*d*) between no. of responses at 10 cm. and at 28 cm., $\chi^2=3{\cdot}2$, df.$=1$, $\cdot 10>P>\cdot 05$.

(All values cited for χ^2 include a correction for continuity).

(ii) The differences in times of first movements towards the stimulus were not significant at the ·05 level in terms of the Mann-Whitney 'U' test, for all comparisons.

Experiment 5. Comparison of Intermittent Stimuli Involving the Same Amount of Light Distributed Over Different Areas

Method

In this and all experiments subsequently reported in this paper, a slight change was made in the method of keeping the chicks after hatching. Hitherto, the newly hatched chicks were placed in a cardboard box, the floor of which was lined with packing material. This box was kept in the darkened drying drawer of the incubator and removed to another heated enclosure nearer the experimental room at the time of testing. The

Table IV.

Diameter of stimulus	7 cm.	10 cm.	15·3 cm.	28 cm.
No. of responses	2 (1M.1F)	5 (2M.3F)	13 (6M.7F)	12 (6M.6F)

innovation was the introduction of compartments into the cardboard box so that there was, after the time of hatching in the incubator, a reduction in bodily contact between the chicks.

The enclosure described in Experiment 1 was used. In one end an aperture 12 inches × 12 inches was cut and covered with plain white, translucent paper which was stretched taut and served as a screen. Light from a projection lantern, fitted with a 150 watt frosted bulb, was focussed on this paper so as to give either a 6 inch circular disc or a 2 inch circular disc., i.e. the same amount of light distributed over a different area. These 'discs' were clearly visible through the 'screen', i.e. from inside the enclosure. An interrupting device in a distant basement ensured that the light was alternately 'on' and 'off' for ½ a second. To human observation, the above arrangement excluded the 'Gamma' movement noted in Experiments 2 and 3. Chicks from two batches were distributed evenly between the presentations at the different diameters. Fourteen chicks were presented first with the 6 inch disc and subsequently with the 2 inch disc and another fourteen in the reverse order. Measurements with a barrier layer cell on the side of the translucent screen facing the chick gave a light intensity of ·03 foot candles for the 6 inch disc and ·24 foot candles for the 2 inch disc. Chicks were exposed to the stimulus for 6 minutes. Consistent approach for two-thirds of the distance was scored as an approach.

Results

The number of chicks approaching each diameter is given in Table V.

The difference in number of chicks approaching the two discs at second presentation was not significant ($\chi^2=0{\cdot}762$, df.$=1$), $\cdot 50>P>\cdot 30$ indicating that the small difference in visual angle involved was not crucial, when the total amount of light was the same.

Experiment 6. Comparison of Intermittent Stimuli of the Same Diameter but Different Intensity

Method

The apparatus used in Experiment 5 was again used; but neutral filters were inserted in the beam to ensure a difference in intensity which was immediately obvious to a human observer. The diameter of the disc of light was 6 inches and once again the light was 'on' for ½ second intervals. The 'bright' disc gave a reading via barrier layer cell and photometer of ·36 foot candles and the 'dull' disc of ·002 foot candles, both readings being taken on the surface of the translucent screen, inside the enclosure while the light was continuously 'on'.

Twenty-nine chicks from 2 batches were exposed for 6 minutes to the stimuli, 14 once only to the intermittent 'bright' disc and 15 once only to the intermittent 'dull' disc.

Results

The number of chicks approaching each stimulus is shown in Table VI.

Table VI.

Stimulus	No. of chicks approaching	
	Yes	No
Bright 6 inch disc	14 (7M.7F)	0
Dull 6 inch disc	6 (4M.2F)	9 (4M.5F)

These proportions by Fisher's Exact Probability Test, give $P=\cdot 00049$ under H_o, or in terms of the Finney (1948) Tables, significance beyond the ·005 level, indicating that intensity is crucial.

Experiment 7. Comparison of Effectiveness of Intermittent Stimuli of Different Colour

Method

The apparatus was the same as used in Experiments 5 and 6 except that Wratten colour

Table V.

Stimulus	1st presentation		2nd presentation	
	Yes	No	Yes	No
Dia. 6 inches	10 (6M.4F)	4 (2M.2F)	12 (6M.6F)	2 (2M)
Dia. 2 inches	10 (5M.5F)	4 (3M.1F)	9 (5M.4F)	5 (3M.2F)

Table VII.

Approach	To red	To green	To white	Total
Yes	8 (5M.3F)	7 (4M.3F)	6 (3M.3F)	21
No	11 (6M.5F)	12 (7M.5F)	13 (9M.4F)	36
Total	19	19	19	57

filters and neutral filters were inserted in the beam of the lantern to give coloured discs of the same intensity. As indicated by barrier layer cell and photometer, the intensity of all stimuli was ·43 foot candles and the colours were: Red (via Wratten filter 29), Green (via Wratten Filter 61) and White. The diameter of all stimuli was 6 inches and the duration ½ second on/off. The centre of the circle of light was 6 inches above the surface of the table. The chicks were exposed to the stimulus for 8 minutes. Equal numbers from each batch were presented to all three stimuli. Consistent approach for two-thirds of the distance of 4 feet was scored as an approach.

Results

The number of chicks approaching each stimulus is shown in Table VII.

No significance is indicated ($\chi^2 = \cdot 45$ for df. 2, $P = \cdot 80$).

Experiment 8

While significant differences were not obtained in the number of approaches to intermittent, coloured lights, it was thought advisable to test the responses to coloured balls moving away from the chick and to determine if greater differences in visual angle were important.

Method

The spheres were suspended from a rotating arm in a circular run so as to have the centres 4 inches (low position) and 15 inches (high position) above the floor on which the chick stood. The balls were 4 inches in diameter and coloured Red, Green and White, the nearest match on the Munsell Colour Chart being Red, 5.0R, 5/12; Green, 2.5G, 6/6; and plain white respectively. The ball was placed 2 inches in front of the chick and the rotating arm moved slowly forward for 6 seconds—stopped for 6 seconds—moved for 6 seconds and so on. Some slight lateral movement of the balls was inevitable. The chick was judged to have followed the ball if it had passed an arbitrary point representing a distance covered of approximately 5 feet. As nearly as possible, equal numbers from four batches were allotted to each colour and position.

Results

Table VIII.

Colour, irrespective of position				
Approach	Red	Green	White	Total
Yes	6	5	3	14
No	11	11	13	35
Total	17	16	16	49

$\chi^2 = 1 \cdot 148$ for df.$=2$, $\cdot 70 > P > \cdot 50$.

Table IX.

Position, Irrespective of Colour.			
Position	Approach		Total
	Yes	No	
Low	12	13	25
High	2	22	24
Total	14	35	49

$\chi^2 = 7 \cdot 597$ (corrected for continuity) for df.$=$ 1, $\cdot 01 > P > \cdot 001$.

The foregoing results, in respect of colour, as with those of Experiment 7, are not significant, but it may be noted that although the experimental design was different, the results are in the same direction. By comparison, the significant results for 'low' and 'high' presentations suggested that the height of the stimulus above the chick is a much more important factor and led to the next experiment.

Experiment 9. Response to Intermittent Stimuli at Different Heights, i.e. Different Angles of Regard

Method

A 'run' similar to that described in Experiment 5 was used. Light from a projection lantern out-

side the enclosure was focused to give a 3 inch disc of light intermittently on/off for ½ second of intensity 1·4 foot candles. The flashing 3 inch disc was presented with centre 2 inches (low position) and 20 inches (high position) above the table by raising the lantern. The chick was placed inside the enclosure, 45 inches from the translucent paper on which the light was flashed and with ample space behind it to permit retreat. The difference in angle of regard for the chick between high and low position was approximately 21°, 30′. Twenty chicks first encountered the flashing disc at the 'low' position and approximately 15 minutes later at the 'high' position; 18 chicks were similarly treated, being presented first with the 'high' position. The time allowed for response was 6 minutes and consistent approach for over half the distance was scored positively.

Results

Table X.

Approach and fixation	1st presentation		2nd presentation	
	Yes	No	Yes	No
To Low position	14 (7M.7F)	6 (2M.4F)	15 (7M.8F)	3(2M.1F)
To High position	2 (1M.1F)	16 (8M.8F)	9 (4M.5F)	11 (5M.6F)

For the first presentation $\chi^2=11{\cdot}2$ (corrected for continuity), df.=1, $P<{\cdot}001$, and for the second presentation $\chi^2=4{\cdot}44$ (corrected for continuity), df.=1, ${\cdot}05>P>{\cdot}02$. The median time of first movement for the 14 which moved to the 'low' position at first presentation was 27 seconds with a range of 10 to 220 seconds. The two chicks which moved to the 'high' position moved first at 70 seconds and 175 seconds. The median time of first movement to the 'low' position at second presentation was 20 seconds with a range (4-140) seconds and to the 'high' position 36 seconds and (4-116) seconds respectively).

It is worthy of note that 14 chicks which failed to run to the 'high' position at first presentation did run to the 'low' positions. Only one which failed to run to the 'low' position at first presentation subsequently ran to the 'high' position, although 7 which ran to the 'low' position first, subsequently ran to the 'high' position. Three instances were noted of the chick approaching the 'high' position with the beak pointed upward towards the stimulus.

Experiment 10. Attachment to Intermittent Stimuli in a Situation Involving Choice

The present experiment was designed to test whether or not intermittent stimuli could promote a degree of attachment comparable with that reported in studies of 'imprinting'.

Method

A rotating white disc, 12 inches in diameter with a black sector 45° painted on it was placed at one end of a test run. The speed of rotation was one revolution per 1·5 seconds. Six chicks which approached the disc at the first trial were allowed a further two 'approaches' and thereafter, for a total of seven days, three training approaches at approximately the same time each day. Another six chicks were similarly treated in the same run with a flashing disc of light as the stimulus. The disc was 6 inches in diameter with centre 6 inches from the floor, 'on' for ½ second and 'off' for ½ second, and with an intensity as measured by a barrier layer cell on the surface confronting the chick of ·5 foot candles. The chicks were allotted to each group in equal numbers from three batches. After the first trial they were kept in heated and lighted boxes in visual isolation from other chicks. On the eighth day, the chicks were confronted with a choice situation. On the open floor of a large room, hitherto not used in the experiment, the angular points of an equilateral triangle with sides of 10 feet were marked. The chick was placed at one angular point and one of the stimuli at each of the other points, facing the chick. It was thus possible for the chick to see and approach either stimulus. Two trials were permitted, with the stimuli on alternate sides (i.e. at the angular point to the left and to the right) of the chick. Both stimuli were silent in operation. The room was darkened but the rotating sector was illuminated as in the trials during the week.

Results

In all cases, the chicks moved towards the familiar stimulus which they had approached during the week and remained in its immediate

vicinity even though the other stimulus was at the same time clearly visible to them. Contentment chirps and pecking, on the way, and in the vicinity of the stimuli were noted in 9 cases. Tested by the Fisher Exact Probability test, the data as set out in Table XI, indicate that approach by 12 chicks to the familiar stimulus

Table XI.

	Familiar stimulus	Unfamiliar stimulus	Total
Actual approaches	12	0	12
Null hypothesis	6	6	12
Total	18	6	24

$P = \cdot 00686$ under H_0.

would occur very rarely by chance and would suggest that intermittent stimuli operating at one point in space can promote an effective degree of attachment. The average time of first movement to the rotating disc was 1 minute 56 seconds and to the flashing light 1 minute 46 seconds. The average times taken to complete the distance to the stimuli on the first run, were 2 minutes 40 seconds and 2 minutes 56 seconds respectively. The differences in both cases were not significant at the ·05 level, applying the Mann Whitney 'U' test.

Discussion

Response to intermittent visual stimuli would appear to be subject to considerable individual differences. Failure to respond within the arbitrary time-limit of the experiments may take the form of no movement at all, short and fitful movements towards the stimulus, or indefinite movements on the base line. Some chicks do respond strongly with the complete pattern of movements after initially turning away, and a strong effort to respond is apparent in some chicks with considerable deformation of the feet.

While the results here reported do indicate that some features of the stimulus situation are more significant than others in inducing the initial movement of approach, our observations would suggest that exclusive attachment to a particular stimulus is not a sudden and irrevocable development.

The negative results in respect of colour could be compared with those reported by Hess (1959) in a different experimental design, namely that Vantress broiler chicks, as tested by discrimination experiments, 'imprinted' more readily on coloured spheres moving away from them, in the order, from highest to lowest, blue, red, green, orange, grey, black, yellow, white.

The considerable differences in the responsiveness of batches, even at the same season of the year, remains a problem.

Summary

Experiments to define further the visual properties of the stimulus situation associated with initial approach by the domestic chick, indicate:

1. Vertical and horizontal movement in a distant intermittent stimulus do not differ significantly in effectiveness.

2. Within the range of 1 cm. to 28 cm. the diameter of the distant intermittent stimulus was found to be a significant variable and appears to be associated with the total amount of light involved in the visual stimulus which, within the limits used, was found to be very significant.

3. Differences in colour (Red, Green and White) of distant flashing lights were not found to be significant.

4. Differences in colour of spheres (Red, Green and White) moving away from the chick were not found to be significant; but were in the same direction (Red and Green slightly better than White) as those for distant flashing lights.

5. The angle of regard (height of stimulus above the chick), both for spheres moving away from the chick and for distant intermittent stimuli, was found to be a crucial variable.

6. Distant intermittent stimuli (flashing light and rotating black (45°) sector on white background) can be associated with a significant degree of attachment in a situation permitting discrimination.

REFERENCES

Fabricius, E. (1951). Zur Ethologie junger Anatiden. *Acta Zool. Fenn.*, **68**, 1-175.

Finney, D. J. (1948). The Fisher-Yates test of significance in 2 × 2 contingency. *Biometrika*, **35**, 149-154.

Hess, E. H. (1959). Imprinting. *Science*, **130**, No. 3368, 133-141.

Hinde, R. A., Thorpe, W. H. & Vince, N. A. (1956). The following response of young coots and moorhens. *Behaviour*, **9**, 2-3, 214-242.

James, H. (1959). Flicker: an unconditioned stimulus for imprinting. *Canad. J. Psychol.*, **13**, 2, 59-87.

James, H. (1960). Progress Report: N.R.C. Grant A.P.A. —37, in a personal communication.

Koffka, K. (1935). *Principles of Gestalt Psychology*. London: Rutledge & Kegan Paul.

Lorenz, K. Z. (1957). The companion in the bird's world. *Auk*, **54**, 245-273.

Ramsay, A. O. & Hess, E. H. (1954). A laboratory approach to the study of imprinting. *Wilson Bull.*, **66**, 157-234.

Siegel, S. (1956). *Nonparametric Statistics in the Behavioural Sciences*, pp. 96-104. New York: McGraw-Hill.

Smith, F. V. (1960). Towards a definition of the stimulus situation for the approach response of the domestich chick. *Anim. Behav.*, **8**, 3-4, 197-200.

Accepted for publication 31*st March*, 1961.

THE INFLUENCE OF IMPRINTING ON THE AGONISTIC AND COURTSHIP RESPONSES OF THE BROWN LEGHORN COCK

By PHILIP GUITON

A.R.C. Poultry Research Centre, Edinburgh

I. Introduction

The influence which early social experience can exert on the development of sexual behaviour was first recognized by Whitman, working with doves, according to whom:

> 'If a bird of one species is hatched and reared by a wholly different species, it is very apt when fully grown to prefer to mate with the species under which it has been reared.' (Whitman, 1919).

Hand-reared birds were found by Heinroth (1910) and by Craig (1914) to develop strong sexual fixations to humans. Heinroth found this with a number of species, and drew attention to the importance, especially among the Anatidae, of the very first social contacts made by the newly hatched young. Lorenz (1935, 1957) extended the study of these phenomena, and was led to postulate that for many species of birds, species-recognition by the individual is determined during a short critical period of infancy which coincides or overlaps with the period during which it learns to recognize its parents. He further proposed that this time-restricted process of determination, called Imprinting, is irreversible: the imprinted stimuli continue to exert an effect on behaviour (e.g. on mating) throughout life; they are more effective than any other, and no later readjustment is possible, even if the animal has been imprinted with a different species.

This theory is a possible, though not a necessary, conclusion from the data, which relate to animals reared or imprinted with an abnormal object or foster parent, that is, reared in an abnormal or deficient social environment. Such a situation might result not only in a specific determination of the stimuli for social behaviour patterns, but also in a distortion of the developmental processes which could make difficult or impossible later stages of development or adjustment. It is significant that infantile food-begging responses are more commonly retained in adult life by hand-reared birds—especially those reared in isolation—than by wild ones (Meyer-Holzapfel, 1939; Kramer, 1957). This infantilism, markedly influenced by the method of rearing, is not apparently associated with physiological or somatic abnormalities, and would seem to depend on the hypertrophy of the neurophysiological response mechanisms (Kramer, 1957). Analogous hypertrophy of infantile imprinted reactions might cause them to persist in the adult bird and influence its social behaviour.

The phenomenon is no less interesting for the possibility that it may reflect an abnormal course in the development of behaviour, especially as a critical period for the development of social relations has been described in human infants (Spitz & Wolf, 1946; Goldfarb, 1947; Bowlby, 1951; Gray, 1958); and its experimental verification and analysis in animals might be expected to throw light on certain problems of human behaviour.

Except for a recent study with turkey poults (Schein & Hale, 1959), no controlled experiments have previously been carried out on the long-term effects of neonate imprinting. Few data are available on even such a basic question as what proportion of imprinted individuals (of a given species) continue to be affected by the imprinting object in adult life. Furthermore, in many reports the possibility is not excluded that long-term effects may depend on repeated contact between subject and object after the initial period of exposure. This is a particularly important point should imprinting be a self-reinforcing process, for repeated exposure to the stimulus might then be expected to lead, not to the extinction of the response, but to its reinforcement.

This paper contains an account of some experiments carried out to study the possible influence of neonate imprinting on intraspecific patterns of behaviour in the adult male domestic fowl. An earlier indication that such an influence might exist was provided by the fact that testosterone-injected White Leghorn chicks, hand-reared in isolation from one another, were found to react sexually to the human hand when 24 days old (Noble & Zitrin, 1942). Preliminary tests confirmed these observations.

2. Experiments

General Procedure

The method of rearing the birds was in the main similar to that which had been used in previous experiments (Guiton, 1959). Twenty-four hours after hatching each male chick was transferred from its hatching box in the incubator to an individual cage and provided with food and water. Except for isolated birds (see Group I), they were transferred at about 40 hours of age to a communal brooder. Chicks trained to follow an object were moved after the first training session. The temperature of the brooder room was maintained at 37°C. until the third day after hatching, and then very gradually reduced. By the 5th week the birds were transferred to a larger and unheated brooder.

Between the ages of 8 and 12 weeks all cockerels were housed together in a large pen, but then again moved, this time to individual wire-sided and wire-floored cages, in order to prevent fighting.

Imprinting Models

Two models were used: model T, a triangular box 35 cm. long at the base, 18 cm. high, and 12 cm. broad, with green sides, and brown ends, and orientated so that the apex of the triangle was nearest to the ground; and model R, a rectangular box 27 cm. long, 12 cm. high and 12 cm. broad, with blue sides and orange ends and underside. Both models had a ground clearance of about 7 cm. when suspended in position from an overhead rotating arm which drove them around an arena 180 cm. in diameter at an approximately constant speed of 18 cm. per second. Each model also contained a speaker connected by overhead leads to a tape-recorder.

Training

The chicks were imprinted by training them to follow one or other of the two models, during daily sessions of about one hour, on the 2nd, 3rd, 4th and 5th days after hatching. For a given bird the same model was used at each session. The bird was placed in the arena just in front of the model, which was then continuously driven round for the duration of the session, while at the same time a recording of a broody-hen clucking was played through the speaker in the model, in the repeated sequence: 12 seconds on and 18 seconds off.

Testing

Birds were tested singly, in the same arena as was used for training, but the bird was placed in the centre equidistant from the two models (T and R) which were suspended at diametrically opposite points of the arena. The motor driving the overhead rotating arm was then started, and the response of the bird to this choice of two moving models was recorded. During these tests the models were silent.

Trained chicks (Groups I and II, see below), were tested with models T and R when 7 days old, and again when 3, 6, 8 and 24 weeks old. Untrained control birds (Groups III and IV) were tested in the same situation at 6, 8 and 24 weeks of age. Some of the birds were also tested at 12 and 16 weeks of age. and again when 9, 10, 12 and 14 months old.

In addition, certain of the birds were tested when ten months old in a choice situation, consisting of the training model for that particular bird and a stuffed cockerel; and again at 14 months old with the training model and a stuffed hen.

All tests lasted 10 minutes, except those carried out when the birds were 8 and 12 weeks old, and they lasted for 20 minutes.

Treatment Groups (Table I)

Chicks were either trained to follow a model individually (Group I) or communally, five at a time (Group II). Within each of these two groups some chicks were trained with the one model and some with the other. With the exception of 7 chicks of Group I which were individually caged for the first 7 days, all the trained birds were reared in brooders containing, for the first 7 days, duplicates of their respective training models. From the 8th day all were communalized in a brooder, without duplicates of the training models. In contrast to the rest of the trained birds of Groups I and II, the 7 birds individually caged at the beginning were therefore visually deprived of their respective models during a large part of the training period. Except where otherwise stated, however, they have been included with the other individually trained birds as a single group.

Control chicks not trained to follow a model were habituated to the experimental test situation a few days before they were first tested at 6 weeks old (Group III). These birds were placed in the arena three or four at a time, and left there for 2 hours 30 minutes, in the presence of a moving but silent model, either T or R. This

Table I. Experimental Treatment Groups

Group	Type of treatment	Age at	No. of treatment sessions	Duration of sessions	Total	No. of birds in	No. of birds treated with:	
							Model T	Model R
I	Trained individually to follow model	2nd-5th day inclusive	4	1 hr. & 15 min.	5 hrs.	17	9	8
II	Trained communally to follow model	2nd-5th day inclusive	4	1 hr. 25 mins.	5 hrs. 40 mins.	10	5	4*
III	Habituated with a model	6th week	3	2 hrs. 30 mins.	7 hrs. 30 mins.	7	3	4
IV	Habituated without model	6th week	1	2 hrs. 30 mins.	2 hrs. 30 mins.	4	0	0

*One bird died soon after the training.

was repeated on 3 successive days, the same model being used for the same birds on each occasion. Four other birds (Group IV) were given a single habituation session, 2 hours 30 minutes long, without either model being present.

A comparison can be made of the behaviour, in the simultaneous choice tests, of birds which had been trained with model T with that of birds trained with model R. This within-Group comparison would alone be sufficient to test the hypothesis that adult sexual responses are influenced by imprinted stimuli. Moreover, it could be expected to expose any effect due to accidental incorporation into the model of specific inborn stimuli: if, for instance, an overall bias existed in favour of one or the other models (Jaynes, 1956; Guiton, 1959). The inclusion of Group III covered the further possibility that imprinted birds might show a great deal of stimulus-generalization of their previous experience. Comparison of the behaviour of trained birds with that of habituated birds might in addition, show to what extent, if any, social responses to the models in the tests were influenced by the degree of fear, either of the situation as a whole, or of the unfamiliar model. Group IV were just sufficiently habituated to make them docile enough to test.

Previous observations had suggested that imprinting was very much less effective if the birds were trained communally to follow a model than if trained individually. Hence, the comparison of Groups I and II should provide a further means of assessing the importance of the degree of relation between infantile imprinting and sexual behaviour.

Classification and Measurement of Behaviour

(1) The Following Response

The total amount of time which a bird spent walking in the same direction as the model was moving and within 30 cm. behind it or 15 cm. in front of or to either side of it, was measured in all tests. This value may be taken as one indicator of the strength of imprinting. The proportion of this time which it spent following the correct (training) model—the level of discrimination—is another.

(2) Aggressive Behaviour

This was classified according to the degree to which aggression was clearly recognized in the response.

(*a*) *Attacks:* the bird ran towards the model, usually with trailed or beating wings, and then either struck it with bill or spurs (or attempted to do so), or postured threateningly at the model. In threat the body tends to be ballooned by erection of the feathers, especially in the breast region, the wings are trailed a little, and the neck sits well down on the back.

(*b*) *Aggressive approach:* the model was approached, usually more slowly than in attacks, in an erect posture, the head held high with the bill directed downwards, and the feathers sleeked except on the nape, but the bird rarely struck the model.

(*c*) *Attack-avoidance:* the bird rushed at the model, lowered its head on arriving near to it, and dodged this way and that, then finally fled.

The frequency of these three responses was measured.

(3) Displays

Waltzing and tidbitting have both been described elsewhere (Davis & Domm, 1943; Wood-Gush, 1956). They are the two most distinct displays in the domestic chicken and commonly occur in both sexual and agonistic encounters. Tidbitting also occurs in other situations: broody hens call chicks to a source of food by tidbitting; and it may also be performed by birds from 5 weeks of age upwards, when they feed, though usually in a less intense and less sustained form. Tidbitting moreover, is not always precisely orientated to another bird, so that this pattern is a less satisfactory indicator of either sexual or agonistic behaviour than waltzing. The frequency of both these activities was recorded.

Semen production. Brown Leghorn cockerels become fertile at about 20 weeks old. Ten of the birds, 5 imprinted and 5 non-imprinted, were tested by manual means for semen production 3 days before the behaviour test at 24 weeks old. Semen was recovered from all 10 birds.

3. Results

The Following-response

The mean duration of following at 7 days and at 3, 6 and 8 weeks, of T- and R-trained birds in both Groups I and II, is shown in Fig. 1. The great difference in the amount of following between the birds of Groups I and II at 1 week old is evident (Fig. 1). Only one bird in Group I followed for less than one minute, whereas no bird in Group II followed for more than 53 seconds. Furthermore, the birds of Group I, with a single exception, had a very marked preference for the correct model—a preference of 96 per cent. or more in 15 of them, while those of Group II showed much less clear discrimination. In fact, though a preference for the correct model was registered at 7 days by the 8 birds of Group II which followed at all, the total scores for this response are so low as to throw some doubt on the significance of the discrimination.

These differences between birds in Group I persisted in subsequent tests, although in both groups there was a strong tendency for the

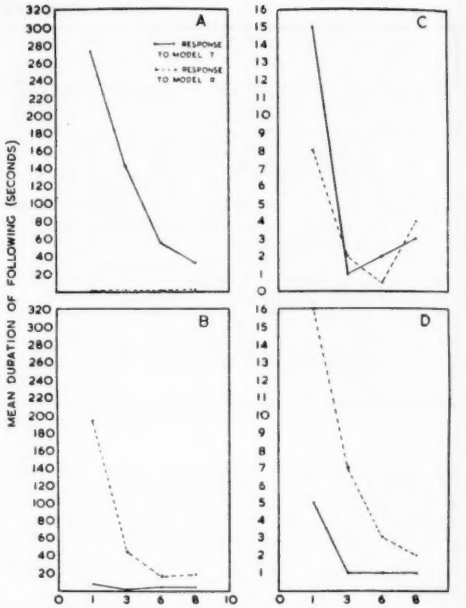


Fig. 1. The following-response of birds individually (A) and communally trained (C) with model T, and of birds individually (B) and communally trained (D) with model R. Note the difference of the ordinate scales of A and B compared with C and D; abscissa gives age in weeks.

scores for duration of following to become progressively reduced in successive tests in those individuals which still responded (Fig. 1) and an increase in the number of birds which ceased to respond. By the time the birds were 8 weeks old, 3 birds in Group II still showed signs of following, though only 2 of them preferred the correct model, whereas the majority of Group I still responded, all discriminating correctly (Figs. 1 and 2). At 12 weeks 4 of 10 tested birds in Group I still followed a little, but none of the 9 birds in Group II did so.

There was no appreciable difference within Group I between the means of the following scores (duration and discrimination) for the 10 communally reared chicks and the 7 reared in isolation. None of the habituated birds (Group III) and none of the birds in Group IV showed any sign of following either model when tested at 6 and 8 weeks old, or after.

These comparisons leave no doubt that the following-response at 7 days and after was

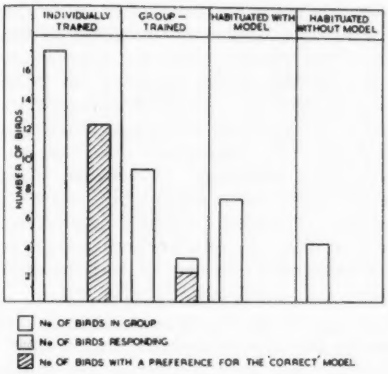


Fig. 2. The number of birds in each Group which followed a model, and the number which correctly discriminated, when 8 weeks old.

determined by the model with which a bird had been trained, and that the degree of imprinting as assessed in this way was very markedly less in the case of chicks trained to the model in groups of five than in individually trained chicks.

No reliable evidence was found of an inborn preference for a particular model. In Group I, the mean following score of T-trainees at -7days old was higher but not significantly different from that of R-trainees ($P=0{\cdot}2$), and there was no apparent difference between them in the degree to which they preferred the correct model. As to the Group II birds, the differences were negligible, and, in any case, in the reversed direction (Fig. 1).

Aggression

A few of the birds in Groups I and II were aggressive at 6 weeks old, but aggression only became marked at 8 weeks. By the time the birds were 12 weeks, however, no aggression was seen. At 24 weeks no attacks occurred, a negligible total of only 5 pecks (among 4 individuals) being scored for all 36 birds tested.

The frequency of aggressive responses at 8 weeks among the birds of different groups is shown in Table II. Aggression was largely confined to birds which had been trained to follow a model (Groups I and II). The mean number of aggressive responses per bird in Group I was significantly higher than that in Group III ($t=3{\cdot}273$; for 22 d.f., $P<0{\cdot}01$); and the mean number of responses in Group II was higher than that in Group III ($t=3{\cdot}090$; for 14 d.f., $P<0{\cdot}05$). The difference between Groups I and II was not statistically significant.

The aggressively responding birds of Groups I and II showed evidence of discriminating the training and the unfamiliar models (Fig. 3).

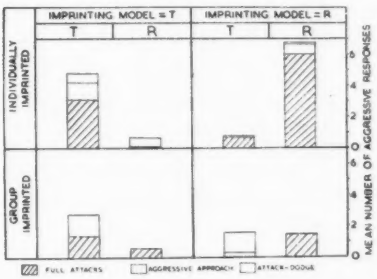


Fig. 3. Aggressive responses to the models in Group I and Group II birds when 8 weeks old.

R-trainees responded more frequently to model R than to model T, while T-trainees preferred model T ($X^2=4{\cdot}381$. $P<0{\cdot}05$). Although this discrimination seemed more pronounced in the individually trained birds (Group I) than in the communally trained ones (Group II) the difference is not statistically significant except for those birds trained with model R ($X^2=7{\cdot}2828$, $P<0{\cdot}01$).

Table II. Mean Number of Aggressive Responses to the Simultaneously Presented Imprinting and Non-imprinting Models at 8 Weeks Old.

Treatment and group	Imprinted		Habituated to experimental situation	
	Individually (Group I)	In groups (Group II)	With model (Group III)	Without model (Group IV)
Mean no. of responses	5·88	3·66	0·57	0
No. of birds in group	17	9	7	4
No. of birds responding	11	7	3	0

Within Group I there was no apparent difference, in either frequency of aggressive reactions or in the degree of discrimination, between the 7 birds reared in isolation during the training period and the other 10 birds reared communally.

There is no evidence of an inborn preference for either model. In Group I—individually trained birds—more T-trainees than R-trainees showed aggression, but the frequency of aggressive acts per responding bird was greater among the R-trainees (Fig. 3). The latter difference in favour of model R is also, it should be noted, in the reverse direction to that found for the following-response. The differences found within Group II are negligible.

The effect of training on the occurrence and distribution of aggressive acts suggested by these results is to some extent supported by the fact that, of those birds in Group I in which there was very little or no aggression at all, two were still following the model in a very chick-like fashion at this time, and were physically backward, with undeveloped combs, two had shown evidence of only weak imprinting from the first, and the others had already ceased to follow the model at 3 weeks old, that is, before the first occurrence of overt aggression towards the models.

Displays

Tidbitting. This activity occurred in most birds of all except Group IV. It appeared to occur in the birds as early as 3 weeks old, though the typical call usually associated with the pecking at the ground was at this time given at a higher pitch than in older birds. The call was not invariably accompanied by pecking, either at 3 weeks or in later tests.

There was no difference in the frequency of tidbitting (call alone or call with pecking) between the birds in Groups I, II or III at either 8 weeks (Table III) or 24 weeks. In most cases the activity seemed not to be elicited by or directed at the models, and often occurred as soon as the bird was placed in the test situation before the models had begun to move. In those few cases where the bird appeared to be tidbitting at a model, the bird also waltzed just before or just after doing this. Subsequent observations have shown that tidbitting in Brown Leghorn cockerels often occurs when a bird is given food, or when it is suddenly visually isolated from its fellows, and that it cannot therefore be regarded as a satisfactory criterion of responsiveness in the context of the present experiments.

Waltzing. In all the tests until the birds were 24 weeks old typical waltzing in response to a model was seen only in 3 birds, and repeatedly in only 2 of them (BR and G), but the partial movement at low intensity occurred in 3 more individuals (Table IV). In all cases the birds involved had been model-trained, either individually or communally, and all waltzed to the training model only. The two birds in which the display occurred relatively frequently and repeatedly had both been individually trained, one to model R and one to model T.

Tests of Birds After Sexual Maturity

After the test at 24 weeks, by which time the birds were reproductively mature, six were kept for further study, including the two consistent waltzers (BR and G), 3 other individually trained birds, only one of which had shown some indication of waltzing during a previous test, and one communally trained bird.

Test I. Simultaneous choice test with model T and model R. All six birds tested at 9 months old. Birds BR and G were observed for 5 minutes each during which they waltzed at their training models 18 and 3 times respectively. BR also sometimes pecked at the leading end of its training model at the end of a waltz. Both birds

Table III. Tidbitting and Food-calls at 8 weeks.

Treatment	Individually Imprinted	Group imprinted	Habituated with model	Habituated without model
Mean number of responses	6·2	6·6	7·0	0·25
Number of birds responding	13	8	6	1
Number of birds in group	17	9	7	4

Table IV. The Occurrence of Waltzing in Individual Birds.

Bird	Training condition	Training model	Age (weeks)				
			6	8	12	16	24
W.LB	Grouped	T	0	0	0	(1)T	0
BL.dB	Grouped	R	0	(1)+1 R	0	(1) R	0
W.O.	Individually	T	0	0	(1) T	0	0
B.R.	Individually	R	0	4 R	16 R	7 R	10 R
P	Individually	T	(1) T	(2) T	—	—	0
G	Individually	T	0	(1) T	—	—	5 T

tidbitted, but not obviously to either model. None of the other 4 birds, each of which was observed for 15 minutes, was seen to waltz or peck at either model, though two of them showed a total absence of fear or avoidance of the models. Three tidbitted, but in none was this behaviour clearly directed at a model.

Test II. Simultaneous choice test with the training model (T or R) and a stuffed Brown Leghorn cockerel in place of the non-training model. All six birds tested at 10 months old. Each bird was tested for 5 minutes, and one for a further 5 minutes. In two cases the test was interrupted to prevent the stuffed bird from being destroyed by the bird's attacks. All six birds waltzed to the stuffed cockerel; and all attacked it. Only BR and G waltzed to the training model, though less frequently than to the stuffed cockerel. The waltzes and pecks at the models, in these two birds, were very similar to the responses directed at the cockerel, but generally less intense or sustained. BR and G were also seen tidbitting at their respective training models.

Test III. Three days later birds BR and G were once more tested with models T and R. Bird G did not walt or respond to either model during the 10 minutes it was observed, but BR waltzed 19 times during 5 minutes, all responses being to its training model (R). Waltzes were usually followed by a characteristic peck at or just above the leading end of the model.

Between test III and the next test, the birds were several times exposed to the stuffed cockerel as well as to the models, while being filmed.

Test IV. When they were nearly 14 calendar months old, bird BR and G were given another simultaneous choice test with models T and R. Both birds waltzed several times to their respective training models only, and both tidbitted to the same model, these displays being particularly intensive in the case of bird BR.

Test V. The following day these two birds were tested with their training model together with a stuffed Brown Leghorn hen. G at once began to waltz intensively to the hen and peck at her comb or head, but ignored the model. BR began by waltzing twice to its model (with pecks at the head end), then rushed across to the hen and began to waltz and then to attack it. The attack became so vicious that the test was stopped after 2 minutes and the hen removed. BR then switched its attention to the stationary model R and waltzed round it. The response to the hen was clearly more vigorous, but also relatively more aggressive. Aggressiveness towards females is not uncommon in cockerels reared in the normal manner.

It is concluded that in only two birds (both individually trained) did the effects of training persist after the birds were 8 to 12 weeks old. In these two, there is little evidence that the behavioural fixation to the training model—expressed as waltzing—showed any definite deterioration, at least up to the age of 14 months, in spite of several exposures to a stuffed Brown Leghorn cockerel and hen. More intensive responses, as regards both waltzing and aggression, were, however, elicited by the stuffed birds than by the model.

Flight and Avoidance

Table V shows the number of birds in each group which showed no sign of fear whatever when repeatedly touched or pushed by one or both models. Only cases of extreme docility have

Table V. Number of Birds in Each Group Showing no Avoidance of Models at 8 weeks and 24 weeks old.

Group	No. of birds in group	No. of birds not avoiding models	
		8 weeks	24 weeks
I	17	5	10
II	9	3	5
III	7	0	2
IV	4	0	0

been included. The difference in the proportion of docile birds between Groups I and II on the one hand, and Groups III and IV on the other, suggests that the training to which the birds of the first two groups had been subjected may have affected their degree of fear of either one or both models, even after other social responses had ceased. Of greater significance, however, is the clear indication that an apparently total absence of fear of the models was not a sufficient condition for sexual or aggressive responses to occur.

4. Discussion

The Effect of Training on Juvenile Behaviour

Individually trained chicks (Group I) showed a strong and highly selective following-response to the training model in subsequent tests. Their behaviour towards the model was in other respects also that which could be expected from a chick towards its mother: distress when separated, contentment and greeting calls when united again, and occasional attempts to be brooded by the model; they may therefore be considered to have been imprinted with the model.

The strength of the following-response in these birds decreased progressively over the following weeks, being finally lost by them when they were about 12 weeks old. Since from the age of about 5 weeks Brown Leghorn cockerels begin to develop more adult patterns of intraspecific behaviour—fighting, waltzing and other reproductive responses—the decrease in juvenile behaviour may well have been due, in part, to a change in the mode of response rather than to a specific forgetting phenomenon.

The group trained birds (Group II) were, by contrast, only weakly imprinted, though in some of these too, some juvenile behaviour persisted until they were 8 weeks old. Such behaviour, on the other hand, was never observed in the untained birds (Groups III and IV) during tests when they were 6 and 8 weeks old. Three main types of early experience can therefore be distinguished in the experiments, according to their effects on juvenile behaviour:

(1) individual training to follow a model, leading to strong imprinting:

(2) group training, leading to weak imprinting;

(3) no such training, with no subsequent juvenile responses to a model.

The Effect of Imprinting on Adult Behaviour

Responses characteristic of adult social behaviour, such as fighting and sexual displays, first occur from the age of 5 weeks and onwards in cockerels. During this period, when juvenile behaviour has not yet been entirely lost—the cockerel's adolescence—the training models were found to elicit such behaviour from imprinted birds (Groups I and II), but not from those that were not model-imprinted (Groups III and IV). This clearly shows that imprinting with non-conspecific objects can have an influence on the stimulus mechanisms which later elicit adult reactions, even under normal conditions of rearing which allows extensive intraspecific experience. It is surprising to find that the influence of communal training on later behaviour should have been only slightly weaker than the influence of individual training, since the effectiveness of these two treatments in establishing the earlier following-response was so diverse.

The influence of early treatment appeared to be limited in most individuals to the period of life before juvenile behaviour was entirely lost, and all but 2 birds ceased to react aggressively or display sexually to the imprinting model long before sexual maturity was reached at 6 months. That imprinting can continue to exert its influence on adult behaviour throughout life is indicated by the continued responses of these 2 individuals until they were 14 months old, but it would seem that in most birds the early experience was not by itself sufficient to influence permanently the relevant stimulus mechanisms.

Extensive tests carried out on a sample of the cockerels when they were reproductively mature failed to confirm Lorenz's theory that adult imprinted birds will respond sexually to the imprinting object in preference to a member of the same species. Even those 2 individuals which still waltzed to their training model showed a

preference for a stuffed cockerel or stuffed hen in a choice situation with the model. This contrasts with the findings of Schein & Hale (1959) working with turkey poults. Experiments are being conducted to discover whether these different results are due to the very marked difference between the methods employed in their experiments and those used in the present experiments, or whether a species difference is involved. It may be noted meanwhile that the reaction by the turkey poults, in the experiments of Schein & Hale, in preferring a human hand rather than intraspecific stimuli, may not have depended on immediate neonatal experience, at a time of purely juvenile behaviour, but on later experience and under the influence of sexual motivation.

All the reproductively mature birds reacted well to a stuffed Brown Leghorn bird at the first exposure. Under the social conditions of rearing, therefore, imprinting with models did not appear to interfere in any way with the development of the normally effective intraspecific stimuli. The fact that those birds of Group I which were isolated during the first 7 days of life showed no detectable difference of behaviour in comparison with the rest indicates that the development of the stimulus mechanism involved in adult social responses does not, in Brown Leghorns, depend to any very large extent on experience gained during the bird's first week of life.

In conclusion, it is probable that though the Brown Leghorn cockerel's behaviour is influenced by early experience, neonatal experience during the first 5 days of life sufficient to establish a strong and selective following response is yet not in itself sufficient to have effect as irreversible and drastic on subsequent adult behaviour as those reported to occur in some other species (Lorenz, 1935, 1957). It would also appear that the development of the stimulus mechanisms of adult behaviour does not in this bird entirely depend on experience gained during this early phase of life.

Social Interaction Between Chicks and Imprinting

Ducklings and chicks can be induced to follow a moving object when they will not do so on their own, by placing them in the company of others, already imprinted with the object (Ramsay & Hess, 1954; Klopfer, 1959). This is not surprising in view of the strong attractions that chicks have for one another; the importance of social facilitation in synchronizing the activities of a group (Klopfer, 1959); the reduction of fear and distress in chicks as soon as they are in one another's company; and the imprinting-like nature of the bond which chicks establish with respect to one another (Guiton, 1959). The results of the present experiments indicate that when young chicks are communally exposed to the imprinting object, even at the peak of the critical period of imprinting, social interactions interfere with this process. This is perhaps not true for all cases since this procedure on a previous occasion resulted in a normal level of imprinting in 2 out of 5 chicks. Klopfer (1959) has referred to the biological advantages of the facilitating effects of interactions in a variable population. If the present results are valid, they show that the interactions in effect inhibit imprinting in birds which would become imprinted if left alone with the stimulus-object. The argument cannot, of course, simply be applied to a group of wild chicks with their own dam since in that situation the imprinting value of a fellow chick may be far below that of the parent, whereas in the experiments described the chicks were in competition with a highly artificial model which there is no reason to suppose constitutes an optimal stimulus. It is, however, conceivable that imprinting of young birds with siblings is of great significance in some species (Lorenz, 1957).

During training the chicks in Group II spent less time following the model, and showed less anxiety and distress when separated from it than did those of Group I. They behaved always as a group, and when following usually followed one or two leaders in the manner described by Klopfer (1959). The leadership, however, constantly passed from chick to chick, though some seemed to respond directly to the model more than others. Frequently the group would start following the model, after ignoring it for a time, apparently because they were frightened or disturbed by noise from outside the arena. Similarly individually trained or partially trained birds can often be forced to keep closer to the imprinting model by mildly scaring them. The importance of anxiety in this respect has been demonstrated by Moltz and his colleagues (Moltz, Rosenblum & Halikas, 1959). The relative ineffectiveness of communal training for imprinting may therefore be due partly to the fact that when following, a chick is for some of the time responding to other chicks, not the model—perhaps becoming imprinted with a chick—and partly to the low level of fear or anxiety of these chicks: fear, or removal of fear,

perhaps playing an essential or important role in the process of imprinting.

5. Summary

1. Experiments were conducted and designed to test if Brown Leghorn chicks imprinted to a specific object in the first week of life, would respond socially and specifically to that object later in life.

2. During the 2nd to the 5th day after hatching, chicks were trained to follow a moving and clucking model made of cardboard and having no apparent or intentional resemblance to a Fowl. Two models, differing in both shape and colour, were used, some chicks being trained with one and some with the other. One group of birds was trained individually, and one was trained in groups of 5 chicks at a time.

3. Other birds were not trained to follow a model, but were later habituated to the test situation, either in the presence of a moving model, or without a model, just before they were 6 weeks old.

4. All trained birds were individually tested at intervals, from the age of 7 days until they were 24 weeks old, in a simultaneous choice situation with the training model and the unfamiliar one. Habituated birds were given comparable tests, but starting only when they were 6 weeks old.

5. Some of the birds were given further, similar, tests after they were 24 weeks old, They were also given simultaneous choice tests with the training model and a stuffed Brown Leghorn bird, either male or female.

6. Until they were 8 or 12 weeks old the trained birds tended to follow the models, though to a decreasing extent with age. The habituated birds never responded in this way. The individually trained birds responded more intensively than did the group trained ones, and moreover, their response was much more selective in favour of the training model: they discriminated more. This showed not only that the training had led to imprinting, but that the individually trained birds had been more strongly imprinted than the group trained ones.

7. At 6 weeks and especially at 8 weeks, the imprinted birds tended to react aggressively to the models, in the same way as birds of that age react to their companions. A few also waltzed—a sexual and agonistic display. Responses were more frequent in the individually (strongly) imprinted than in the group imprinted birds, and discrimination was also better in the former. No such responses were seen in the habituated birds. Imprinting thus appears to have had an influence on adult-type responses. However, in all but two birds—both strongly imprinted—reactions to the models virtually ceased from 12 weeks onwards: the influence could not be demonstrated in the reproductively mature birds.

8. Two birds continued to respond by waltzing—but to the training model only—until last tested at nearly 14 months old. Four other birds tested up to the age of 10 months responded well to a stuffed cockerel, waltzing and attacking, but never to the training model. The 2 permanently imprinted birds also reacted to stuffed birds, both male and female, and did so with more intensity than they responded to the training model. Given a choice of model and stuffed bird, they reacted to the latter.

9. The experiments indicate that neonatal imprinting affects adult social behaviour, and also defines the limits of this influence under specified and controlled conditions.

REFERENCES

Bowlby, J. (1951). *Maternal Care and Mental Health.* Geneva: World Health Organisation.

Craig, W. (1914). Male doves reared in isolation. *J. anim. Behav.*, **4**, 121-133.

Davis, D. E. & Domm, L. V. (1943). The influence of hormones on the sexual behaviour of domestic fowl. Chapter in *Essays in Biology*. University of California Press.

Goldfarb, W. (1947). Variations in adolescent adjustment of institutionally reared children. *Amer. J. Orthopsychiat.*, **17**, 449-457.

Gray, P. H. (1958). Theory and evidence of imprinting in human infants. *J. Psychol.*, **46**, 155-166.

Guiton, P. (1959). Socialisation and imprinting in Brown Leghorn chicks. *Anim. Behav.*, **7**, 26-34.

Heinroth, O. (1910). Beiträge zur Biologie namentlich Ethologie und Psychologie der Anatiden. *Verh. V Int. Orn. Kongr.*, Berlin.

Jaynes, J. (1956). Imprinting: The interactions of learned and innate behaviour: I. Development and generalisation. *J. comp. physiol. Psychol.*, **49**, 201-206.

Klopfer, P. (1959). An analysis of learning in young Anatidae. *Ecology*, **40**, 90-102.

Kramer, G. (1957). Social potentialities, their manifestation and hypertrophy. Communication at IVth International Ethological Conference, Freiburg i. Br.

Lorenz, K. (1935). Der Kumpan in der Umwelt des Vogels. *J. Ornithol.*, **83**, 137-213, 289-413.

Lorenz, K. (1957). Companionship in Bird Life. Essay in *Instinctive Behaviour*. Edited by C. H. Schiller. New York.

Meyer-Holzapfel, M. (1949). Die Beziehungen zwischen den Trieben junger und erwachsener Tiere. *Schweiz. Z. Psychol., Anwand.*, **8**, 32-60.

Moltz, H., Rosenblum, L. & Halikas, N. (1959). Imprinting and level of anxiety. *J. Comp. physiol. Psychol.*, **52**, 240-244.

Noble, G. K. & Zitrin, A. (1942). Induction of mating behaviour in male and female chicks following injection of sex hormones. *Endocrinology*, **30**, 327-334.

Ramsay, A. O. & Hess, E. H. (1954). A laboratory approach to the study of imprinting. *Wilson Bull.*, **66**, 196-206.

Schein, M. W. & Hale, E. B. (1959). The effect of early social experience on male sexual behaviour of androgen injected Turkeys. *Anim. Behav.*, **7**, 189-200.

Spitz, R. A. & Wolf, K. M. (1946). The smiling response: a contribution to the ontogenesis of social relations. *Genet. Psychol. Monogr.*, **34**, 57-125.

Whitman, C. O. (1919). Orthogenetic evolution in pigeons. Vol. 3, *The Behaviour of Pigeons*. Edited by Harvey Carr, Carnegie Inst., Washington, Publ. No. 257.

Wood-Gush, D. G. M. (1956). The agonistic and courtship behaviour of the Brown Leghorn. *Brit. J. anim. Behav.*, **4**, 133-142.

Accepted for publication 24*th February*, 1961.

A THEORY OF THE ORIGIN OF SPADE-FOOTED TOADS DEDUCED PRINCIPALLY BY A STUDY OF THEIR HABITS

By ARTHUR N. BRAGG
University of Oklahoma, Norman

The anatomist, Romer (1941, p. 49-50), states the generally accepted evolutionary position of the amphibians among terrestrial vertebrates essentially as follows: 'The amphibians are a defeated group. They were the first of the vertebrates to emerge from the waters onto the lands; but they were not destined to complete the conquest, and at first abundant, they have shrunken into insignificance among four-footed vertebrates.—The reason for amphibian failure —is not far to seek: it lies in the mode of development. The amphibian is still chained to the water. In the water it is born; to the water it must periodically return. There are various devices among living amphibians which have enabled them to circumvent this difficulty to some extent; but these makeshifts have not been particularly successful. The amphibian is conservative in its basic developmental processes. It is, in reality, little more than a peculiar type of fish which is capable of walking on land.' The historical geologist, Miller (1922, p. 215) expresses much the same idea: 'By the close of the Triassic the Amphibians had declined remarkably so that among the land vertebrates, of which they were the ancestors, they never again assumed a position of importance.'

I have no disagreement with these and similar statements, in the context in which they were written; but some of Romer's 'makeshifts' to circumvent the amphibian's still primitive mode of development seem to be exceptions to the general rule as stated. It is the purpose of this paper to emphasize several of these in the spadefoot toads and to present an hypothesis as to how and when they probably arose under the influence of rapidly increasing severity of selection pressure from the environment. This differs from most evolutionary studies in that the emphasis is upon the development of behaviour and habits rather than upon changes in morphology, an emphasis, incidentally, long neglected by all except a few students of both behaviour and evolution.

The spadefoot toads of North America constitute a small group of forms still in taxonomic confusion. For my purpose here I follow Tanner (1939) in recognizing one genus (*Scaphiopus*) divided into two subgenera (*Scaphiopus, sensu stricto*, and *Spea*). The subgenus *Scaphiopus* contains three forms, *holbrooki* (Harlan), *hurteri* Strecker, and *couchi* Baird. *Spea* contains four forms, *hammondi* Baird, *intermontanus* Cope, *bombifrons* Cope, and *multiplicatus* Cope. Several in both groups are usually considered to be subspecifically related to one or more others, and a few herpetologists recognize another subspecies of *Scaphiopus couchi*. Several follow Brown (1950) in elevating *Spea* to generic rank, as originally suggested by Cope. Since this paper is concerned only casually with nomenclature, the names given seem sufficient to delineate the forms used in this discussion without prejudice as to detailed taxonomic views, either of mine or of others. I shall, therefore, henceforth use each name as though it indicated a full species.

Scaphiopus is the American representative of the widely distributed, mostly northern-subtropical family, Pelobatidae (Noble, 1954). The family is usually considered to be Jurassic in origin, but exactly when *Scaphiopus* as a genus arose is unknown (see, however, below). In some phases of external structure, the present-day spadefoots seem closer to the Ranidae than to the Bufonidae but in habits they more closely resemble contemporary *Bufo* than *Rana*. For example, the spadefoot skin is thin and glandular throughout and (except in *Scaphiopus multiplicatus*) has few or no tubercles. The skin of no spadefoot has the dry, wart-like glands of most *Bufo* species and spadefoot skin loses water more rapidly in a dry atmosphere than that of at least some species of *Bufo*. In these respects it is frog-like. But the spadefoot habitat is on land, often far removed from permanent water (toad-like). Also like many species of *Bufo*, the spadefoots avoid desiccation by burrowing habits and almost exclusively nocturnal activity at the earth's surface. In both of these features the spadefoots really out-do the toads. Spadefoot toads may remain underground for weeks at a time in dry weather and almost none are ever voluntarily active in daylight, except occasionally in very humid atmosphere for breeding (Neill, 1959, and others).

In reproductive habits all of the spadefoots

retain the phase of the primitive amphibian pattern emphasized by Romer (*supra cit.*), i.e. all are born in water and to water they must return. But here we note the first difference—their return to water is not periodic but quite erratic, the first of the 'makeshifts' to be emphasized. They typically breed *only* after the soil of their habitat has been suddenly flooded with water, mostly during or after violent or heavy rains, and usually in the temporary pools thus formed. Only *Scaphiopus intermontanus* is suspected of sometimes using permanent water, but even this after sudden flooding of xeric mountain valleys by overflowing mountain streams (Lindsdale, 1938) or after heavy local rains.

The spadefoots' breeding, therefore, is not seasonal in the sense that most physiologists speak of a breeding season in Amphibia. They have no breeding season—only breeding *periods*, and these periods occur locally at *any* season, whenever water suddenly floods their habitat in sufficient quantity, unless they are prevented by other influences such as low temperature at the time. Even if thus inhibited, at least two species (one in each subgenus), *Scaphiopus bombifrons* (Bragg & Smith, 1948) and *Scaphiopus hurteri* (Bragg, 1959), may breed a few days after heavy or violent rainfall if the temperature rises sufficiently.

Physiologically speaking, this of course means that any healthy adult spadefoot must be prepared at all times to breed (unless having just done so); and this, in turn, implies mature eggs ready to be ovulated and sperm present practically all the time in the respective sexes. Hansen (1958) has recently shown this to be true in the eastern spadefoot, *Scaphiopus holbrooki*; and, while we have no *in vitro* observations to prove it, the non-cyclic breeding of other species makes it all but certain in them all. Since pituitary hormones stimulate ovulation in spadefoots, both *in vivo* (Wasserman, 1957) and *in vitro* (Hansen, 1959), the influence of sudden flooding must in some way indirectly reach the pituitary, perhaps through the clasp of the male (Bragg, 1941) but more likely by imbibition of water (Hansen, 1959) or by both influences working together.

Whatever the details may be, with spadefoots if there is no flooding, typically there is no breeding, regardless of the season of the year; with flooding, many spadefoots breed, again regardless of season. I have known three years to pass locally with no breeding activity among a large population of spadefoots although pools commonly used by them remained full for weeks, either because no one rain was sufficient for stimulation or because the only heavy rains came below the critical temperature (9-10°C.) below which no breeding normally occurs. On the other hand, I have seen large numbers of this same population enter these same pools and produce eggs three times in one calendar year, each breeding period occurring during or immediately after heavy rains above 10°C. These were probably not all the same individuals; for it is also known that some female spadefoots fail to enter pools for breeding when they might be expected to do so (Bragg, 1950). Unfortunately, we do not yet know why the females of a given population collectively 'stagger' their activities after local rains; but that they do so is well authenticated.

Some years ago, I noted that this habit of breeding only after rains (or other flooding) was exactly suited to amphibian life in xeric regions (Bragg, 1944-45, 1946, 1950) where most spadefoots live and that it is shared in its main features by species of several other genera living in dry areas. The grassland-limited *Bufo cognatus* Say follows the rains in breeding (Bragg, 1940), as do *Pseudacris clarki* Baird (Bragg, 1943), *Microhyla carolinensis olivacea* (Hallowell) (Bragg, 1943a), and some other Salientia of the grassland regions of North America. In Oklahoma and adjacent regions, I can find no amphibian species whose distribution is *limited* to non-forested regions that does not follow this general pattern of breeding (Bragg, 1946). Even one salamander able to live in the drier grasslands of North America (*Ambystoma tigrinum mavortium* Baird) shows this pattern despite the fact that nearly or quite all other *Ambystoma* species and subspecies are seasonal in their breeding (Bragg, 1956). When all species living in a definite ecological situation differ from others in their groups living elsewhere in so fundamental a function as reproduction, there must be a reason for it. Such habits must in the nature of things, be an evolutionary adjustment to life in this special situation—one of the 'makeshifts' that Romer (*supra cit.*) had in mind. (See also Hesse, Allee & Schmidt, 1937).

In allusion to the type of habitat in which this habit-pattern typically occurs, I have called it the *xeric breeding pattern*. If such naming based upon habitat be permitted, it is logical to refer to the more usual amphibian pattern as *mesic*, this, of couse, being the better known seasonal

and cyclic breeding pattern of the common frogs and toads, typical in more mesic environments. Incidentally, there is still a third pattern which shows some features of each of the others. This I have called the *intermediate pattern*. It is exemplified, in Oklahoma at least, by leopard frogs (*Rana pipiens berlandieri* Baird), *Bufo woodhousei woodhousei* Girard, *Pseudacris nigrita triseriata* (Wied) and others, again illustrating how habit-patterns in breeding tend to follow habitat rather than morphology and, hence, to cut across taxonomic lines. This point has been earlier emphasized elsewhere (Bragg, 1944-45).

Now if we assume that the mesic breeding pattern is the most primitive of the three—as it almost certainly must be unless amphibian nature is grossly misunderstood—it follows that the xeric pattern has been derived from the mesic one during the development of the present-day spadefoots (and also independently by several other forms now living exclusively in the xeric regions of North America). Since it is reasonable to infer that habit-patterns are as truly a product of evolution as is morphology, the specialized patterns presumably arose as an adjustment to changing environments through mutational changes and the sorting influence of Darwinian selection.* If, therefore, we take these generalizations as premises we can appeal to our geological colleagues for information which, when correlated with the above, can give us reasonable deductions as to where, when, and under what influences the xeric pattern of breeding developed in the spadefoots.

It is well known that in late Cretaceous times North America was completely split longitudinally by an epicontinental sea with an equatorial current running northward (Miller, 1922, p. 247). Along the western edge of this sea, the climate was mild and moist as judged by the types of fossil plants such as maples, sassafras, and even figs characteristic of the upper Cretaceous rocks of this region. We therefore visualize many hundreds of square miles of territory in southwestern North America near the close of the Mesozoic era at least as mild and mesic as conditions along our Atlantic seaboard from North Carolina southward are now. Any amphibians living there would therefore be more likely to have the primitive mesic (rather than the specialized xeric) breeding pattern, unless the latter had already developed elsewhere and been brought in by migration. This contingency is considered very unlikely from the early history of the continent as given by geologists.

According to the best information available (Tanner, 1939), *Scaphiopus* arose in this general region. If this be true, it must have come from a primitive pelobatid stock then present there. We therefore postulate a primitive ancestor of the spadefoot toads inhabiting the land just west of the Cretaceous Sea; and, since these animals lived in a mesic environment, and since there is no reason to believe them formerly to have been subjected to xeric conditions (see Miller, 1922, p. 246), we assume them to have exhibited the typical primitive mesic breeding pattern, seasonally cyclic, essentially as in recent mesic forms.

Near the close of the Mesozoic era, rapid geological changes began which continued for thousands of years. These involved massive mountain building all along the western part of the continent (the Rocky Mountain Revolution). The inland sea disappeared and great outwashes from the new mountains partly filled in hundreds of square miles to the eastward (see Schuchert, 1915, p. 920 for a geologically orientated account of this). As the mountains arose and became higher through the early periods of the new era (Cenozoic) they tended gradually to cut off moisture from the Pacific (and perhaps eventually also from the Atlantic) and general mass movements of air currents, now thought largely to control weather over vast areas, must have changed direction till (as today) the whole area became ecologically desert, semi-desert, dry grassland, or desert-shrub (Clements & Shelford, 1939). The spadefoot ancestor thus was faced with the necessity of migrating, changing its habits to meet the new conditions as they occurred, or becoming extinct. It changed and lived as *Scaphiopus* through (1) developing the xeric breeding pattern, (2) developing the habit of burrowing, and (3) becoming almost entirely nocturnal in activities above ground.

The above considerations place the probable origin of *Scaphiopus* early in the Cenozoic era, and this probability is enhanced by the following: fossil spadefoots which were identified as the common, Recent, eastern spadefoot, *Scaphiopus holbrooki*, have been found not long since in pre-Pleistocene deposits in Florida (Affenberg, 1956). They are also known from the Pleistocene there

*Exactly what role (and how) isolation may play in this special case is fascinating to contemplate in view of the modern synthesis idea in evolutionary studies. In the special circumstances cited below *it may have played no part at all.*

(Holman, 1958). Brattstrom (1957) lists *Scaphiopus* as known from the Pliocene to the Recent.

If this species (*Scaphiopus holbrooki*) really had ancestors in the Southwest, time must be allowed for its reaching Florida over the new land vacated by the Cretaceous sea. This would take at least a geological period, and, in all probability more. Furthermore, *Scaphiopus holbrooki* as presently known has the xeric breeding pattern in advanced form although now living under *mesic* environmental conditions. It is almost certain, therefore, that the xeric pattern in spadefoots developed *before* migration to the eastward had advanced very far. Consideration of all these things together makes it extremely probable that the first *Scaphiopus* lived in the Paleocene or Eocene period. It could have been neither earlier nor much later, although we cannot, without fossils, be certain of the exact time.

I therefore conclude that *Scaphiopus* arose practically at the beginning of (or very early in) the Cenozoic era under the influence of a changing environment which was caused by the Rocky Mountain Revolution with the associated changes in climate in the North American Southwest. Admittedly, the evidence is largely circumstantial; but it is internally consistent and it forms a reasonable hypothesis till proved inadequate. In attempting the correlation of the available data on this problem, I have followed the principle so well stated by Bader (1958) namely, that science often is not so much concerned with certainty as with the 'probability that an hypothesis is true'.

To have evolved as postulated, the early ancestor of the spadefoots must have been relatively plastic genetically, i.e. have had a higher than usual rate of mutability in certain chromosomal loci controlling characters upon which selection could work: and the evolutionary rate in modification of its habits probably was relatively fast, how fast would depend upon the rate of climatic change through the early Cenozoic era to the east of the rising mountains. But once the xeric breeding pattern, burrowing habits, and nocturnal activity above ground were thoroughly established in its genotype, such plasticity would no longer give it a selective advantage, and selection would work toward a fixity of genotype containing factors for such characters. Hence, conservatism is to be expected in the habits of adult *Scaphiopus*—and this is *exactly* what is most characteristic about them in their breeding habits (Ball, 1936; Pearson, 1955; Hansen, 1958). As I once put it (Bragg, 1944-45), having found the xeric pattern 'good' for practically all environments to which they have spread from their origin in the Southwest, they have not needed to change its basic features as they entered more mesic habitats. This was what was so puzzling to the early American naturalists of the East who could not understand why *Scaphiopus holbrooki* (the only spadefoot there) was so different in its habits from the other local species of Amphibia in other genera (see for example, Abbot, 1884, who was so puzzled by this spadefoot's loud call).

The xeric pattern of breeding fulfils two great amphibian necessities in a dry climate: it (1) gets breeding started very quickly and (2) accomplishes this at the time of the greatest amount of surface water. This assures getting zygotes into the right places at the right time; but, not having developed even any suggestion of parental care, the adults have then fulfilled their mission in the life cycle. Species survival after this depends upon the larvae hatched from these zygotes. Let us, therefore, turn to the tadpoles. If these cannot survive under the normal conditions, the development of a special breeding pattern in the adults is of no consequence to a species.

Spadefoot tadpoles develop for the most part in shallow, temporary pools, which not only disappear quickly but which are often lacking in sufficient food. The problem facing them on hatching, therefore, is to develop rapidly enough to emerge onto the land before evaporation kills them (Bragg, 1956a). In xeric environments this problem is a severe test of their abilities and, perforce, subjects them to very great selection pressure. Accordingly, unlike the adults, the larvae are (and must remain to some extent) genetically pliable in their evolutionary adjustments in habits. Any mutation that favours them in the least is likely to spread rapidly in the population, and any that is detrimental will be suppressed or eliminated more quickly than in most forms, even if recessive.

Under these conditions it is not surprising to find that larval spadefoots have developed habits and behaviour in many ways different from those of other tadpoles, even in other Pelobatidae.*

These peculiar developments in larval spadefoots include: (1) *the fastest rate of development*

**Pelobates fuscus fuscus* of Europe is an unexplained exception to this rule, at least as adults (Savage, 1942) and probably as larvae. I am indebted to Mr. I. Fuhn of Bucharest, Rumania, for comments on aggregational phenomena of *Pelobates* larvae. I know nothing of their behaviour from personal experience.

known among larval amphibians. The cleavage rate in the embryo is accelerated above the average, at least in *Scaphiopus bombifrons* (Trowbridge & Trowbridge, 1937), and the developmental rate of their tadpoles may allow them to metamorphose in 13-14 days from eggs in exceptionally favourable pools (King, 1960). *Scaphiopus hurteri* sometimes shows a similar rate under peculiar conditions of food supply, the fastest observed being 12-13 days from eggs (Bragg, 1950). In different pools the actual rate varies greatly, depending of course in part on temperature, but also upon food supply (in quantity or kind). (2) *Special methods of securing food, particularly when it is scarce*. These include (*a*) planktonic feeding in *Scaphiopus holbrooki* (Richmond, 1947), *Scaphiopus hurteri* (Bragg, 1959), and *Scaphiopus bombifrons* (Bragg, 1960; (*b*) co-operation in aggregational feeding in *Scaphiopus holbrooki*, *Scaphiopus hurteri*, *Scaphiopus bombifrons* and *Scaphiopus couchi* (Richmond, 1957; Bragg, 1959; Bragg & King, 1960) sometimes social, sometimes asocial in character; and (*c*) predaceous cannibalism in *Scaphiopus hammondi* and *Scaphiopus bombifrons*, and more weakly in *Scaphiopus holbrooki* and in *Scaphiopus hurteri* (Ball, 1936; Bragg, 1944-45, 1950, 1957; Bragg & Bragg, 1959; Orton, 1954). (3) *Social aggregational behaviour* tending to conserve the rapidly disappearing water, in *Scaphiopus bombifrons* and *Scaphiopus hurteri* at least (the so-called 'scooping' aggregations of Bragg, 1959). (4) *Mass social aggregations during early metamorphic stages* after cessation of feeding, from which mass movement of tadpoles in metamorphosis from the water frequently (but not always) occurs; this last is known certainly only in *Scaphiopus hurteri* (Bragg, 1951, 1959) but probably also occurs in *Scaphiopus holbrooki* (see Goin, 1955, p. 58) and, in modified form, in *Scaphiopus bombifrons* (Bragg & King, 1960). Mass movement of very young *juvenile* spadefoots has also been seen (Neill, 1957).

In addition to all of these peculiar phenomena, predaceous beetle larvae, known to be predatory on tadpoles of *Scaphiopus hurteri*, avoid entering social feeding aggregations of this spadefoot (Bragg, 1950a). The aggregations, therefore, must also act as a partial protective device for the tadpoles. Nothing is known as to why.

These phenomena of behaviour have already evolved in spadefoot tadpoles as peculiar and quite specialized adaptations to life in rapidly evaporating pools. We should not be surprised to find, therefore, that other habits serving the same or similar functions should now be developing and that these should first show up in xeric regions. Nevertheless, one such case was so unexpected as not to have been recognized till very recently—so recently, in fact, that we lack observations on several species that probably have it. Its recognition is due primarily to Orton (1954) and in it we can all but *see* evolution of behaviour and habits occurring.

The development of our knowledge of the phenomenon in question (dimorphism in tadpoles of a species associated with different feeding methods) was as follows:

In early taxonomic studies involving larvae of the spadefoots, the tadpoles of *Scaphiopus bombifrons* were distinguished from those of *Scaphiopus hammondi* primarily by a difference in the larval mouth parts, the shape of the head, and cannibalistic habits. These features were correlated in that the flattening of the head (bulging out at the sides) of the supposed *hammondi* tadpole was caused by hypertrophy of the jaw muscles associated with large jaws with a beak in the upper and a corresponding notch in the lower, which was clearly an adaptation for carnivorous feeding, including cannibalism (Wright, 1929; Smith, 1934; and Bragg, 1941a).

Stebbins (1951) was clearly the first to question the distinction of these two species of tadpoles on the basis of these characteristics, although in using them several workers (including myself) had neglected or misinterpreted some of the observations of Gilmore (1924) and of Storer (1925). Stebbins's idea was soon confirmed by Turner (1952) working on *Scaphiopus hammondi*.

Orton (1954) told of finding a single tadpole with the extreme development of the mouth and head region supposedly characteristic of *Scaphiopis hammondi* near the eastern limits of the distribution of *Scaphiopus bombifrons* and hundreds of miles east of the range of *Scaphiopus hammondi*. Since this tadpole was in a museum collection, its interpretation could follow one of two paths: either (1) the collection area as given in the museum records was in error (as sometimes occurs even in the best of museums), or (2) this must be a tadpole of *Scaphiopus bombifrons*. Orton chose the latter alternative. In doing so, she pointed out that *Scaphiopus bombifrons* must be supposed to have two morphologically different types of

tadpoles, the one cannibalistic and the other not. Such dimorphism was not to be expected—in fact it was unheard of in any salientian tadpole thus far described.

Nevertheless, Orton was right, as I very soon confirmed (Bragg, 1957). The phenomenon in question was then followed up with my son (Bragg & Bragg, 1959). There is now no question whatever about dimorphism in the *Scaphiopus bombifrons* tadpole. It occurs. But, since not all populations manifest it, its distribution is peculiar.

From the viewpoint of this paper, its distribution is one of the most interesting points. I live in central Oklahoma well within the range of *Scaphiopus bombifrons*, which is here very abundant. In more than 20 years of study involving hundreds of thousands of spadefoot tadpoles produced in temporary pools in this region, I have never found one of the cannibalistic type and only one that showed the least tendency towards it. On the other hand, in western Oklahoma the cannibalistic form is usually found if carefully looked for (Bragg, 1946a; Bragg & Bragg, 1959), although some generations of tadpoles in specific pools are of only the usual non-cannibalistic kind.

In some pools that have both kinds of *Scaphiopus bombifrons* tadpoles, it is evident that the behaviour of the two is different. The much more numerous non-cannibalistic type commonly (but not always) feeds in aggregations (Bragg & Bragg, 1959; Bragg & King, 1960), but the few cannibals move freely about *outside* such aggregations, occasionally catching, killing and eating another tadpole, although they eat other things as well. Their *growth rate* is also much faster, so that at a given age after the first week or so they are very much larger than their non-cannibalistic companions. There is, as yet, however, no evidence that their *developmental* rate increases, and their progress toward metamorphosis seems to be the same as most others at a given place. More data, however, are needed on this point.

As several workers have pointed out, where such dimorphism is prevalent, some tadpoles are morphologically intermediate between the two types described. I have found pools in western Oklahoma where large samples have failed to reveal the extreme type of cannibal but where non-cannibalistic and intermediate types were common (see Bragg, 1948; Stebbins, 1951; Turner, 1952).

This recent unexpected discovery in *Scaphiopus bombifrons* raises the question concerning other species of *Scaphiopus*—do any others have dimorphic tadpoles? In the many studies on tadpoles of *Scaphiopus holbrooki* and in my own on *Scaphiopus hurteri* and *Scaphiopus couchi*, no evidence of it has been found, although predaceous cannibalism may occur in some (Ball, 1936), and aggregational feeding is common (Richmond, 1947; Bragg, 1959). So far as we know, therefore, dimorphic tadpoles occur only in the subgenus *Spea*. They are certainly known in *Scaphiopus bombifrons* but are very strongly suspected in others of this subgenus.

Only one other form in *Spea* (*Scaphiopus hammondi*) has been studied sufficiently to give some evidence. Some of its tadpoles were known to be cannibalistic long before dimorphism and cannibalism were known in *Scaphiopus bombifrons*. In New Mexico, in 1940, I followed the breeding of both *Scaphiopus hammondi* and *Scaphiopus bombifrons* in several pools during each of two breeding periods. In some of these pools in which only *Scaphiopus hammondi* were heard calling during the night when the eggs were laid, the tadpoles later varied extremely in size at the same age. The largest ones (at least 4 times the bulk of the majority) had the hypertrophied jaw muscles, beak/notch jaw relationship and other characteristics now associated with the cannibalistic *Scaphiopus bombifrons* of the extreme type (Bragg, 1941a). Turner's study from farther west indicated intermediate types and none of the extremes, some coming from areas well west of the understood range of *Scaphiopus bombifrons*. It is obvious that, not then expecting dimorphism, I may have been mistaken in the identification of the New Mexico specimens as *Scaphiopus hammondi*. I still do not think so, for the reason that I found most pools during breeding nights occupied by one or the other of the two species with very little mixing (Bragg, 1941a); i.e. they tended to be reproductively isolated by the attraction of the males' calls to members of their own species at any given pool. If both Turner (with his intermediates) and I (with the extreme cannibalistic type) be correct in our identifications, then dimorphism in tadpoles of *Scaphiopus hammondi* is all but certain; and, whether I was mistaken or not, Turner's intermediates clearly imply it, since his tadpoles came from regions too far west for it to be likely that they might be confused with those of *Scaphiopus bombifrons*.

Now let us return to evolutionary matters in

association with the present distribution of the spadefoots. The subgenus *Scaphiopus* has one species (*holbrooki*) distributed throughout most of eastern United States, from the Atlantic to about eastern Arkansas. From there westward to about central Oklahoma, western Louisiana, and central Texas, this is replaced by the closely related form, *hurteri*. Just barely overlapping to the west and south is *Scaphiopus couchi*, extending well into Arizona and southward far into Mexico. Of the whole subgenus, therefore, *Scaphiopus couchi* is at present the only truly dry-grassland and semi-desert inhabitant.

In contrast, the subgenus *Spea* is typically western. *Scaphiopus hammondi* occurs in southern and eastern California, is interrupted in the deserts of eastern California and Arizona, then occurs again from central Arizona east to west-central Texas and north-western Oklahoma, northward through central Colorado and southward far into Mexico. Its close relative, *Scaphiopus intermontanus*, replaces it in Utah, Nevada and eastern California northward to just into Canada. *Scaphiopus bombifrons* occurs from just inside Canada north of Montana, south into Mexico. It is found in most of Montana, about the north-eastern half of Colorado, south-western North Dakota, about the western half of South Dakota (farther eastward to the south in this state), all but the eastern edge of Nebraska, most of Kansas, about the western two thirds of Oklahoma (although the population is small east of the central part), adjacent New Mexico and western Texas. *Scaphiopus multiplicatus* occurs only in Mexico. (See maps by Conant, 1958, who, however, does not distinguish *intermontanus* from *hammondi*; see also Stebbins, 1951, whose distribution maps differ slightly). *Spea*, in contrast to *Scaphiopus* (subgenera), tends to occupy drier regions. The only real exception is *Scaphiopus couchi*: *and it is in Spea that dimorphism with predaceous cannibalism is developing*. It is perhaps worth noting in passing that within *Scaphiopus*, *Scaphiopus couchi* is, in details of behaviour, more like the western group (*Spea*) than like its closer relatives (for details, see Bragg, 1944-45).

Now if, as earlier postulated, *Scaphiopus* arose in the Southwest, developed its xeric breeding pattern there, and *then* spread out and differentiated into the recent forms, its present distribution indicates a basic early division into an eastern group and a western one (*Scaphiopus* and *Spea* essentially, although *Scaphiopus couchi* remained with *Spea* in the south and west). The conservatism of the xeric breeding pattern, as developed in the early response to progressively drier climate where it was essential, was carried eastward into more mesic habitats where it *was not necessary but did no harm*. Thus, it was not subjected to selection pressure and therefore not changed. In the western grasslands and semi-deserts, however, not only was the xeric pattern still essential but its possession would do little good if the tadpoles could not survive.

The present distribution of dimorphic tadpoles in *Scaphiopus bombifrons* and possibly other members of *Spea* clearly must be the result of a recent further evolutionary change—in other words, a mutation (or a series of them) has occurred quite recently (as evolutionary changes go) and is being established in the western (hence drier) habitats by natural selection: and this change is involved in behaviour as well as in morphology.

At first sight, this postulate may seem absurd, for how can the development of cannibalism, of all things, in a species aid in its survival? But we need only to look again at the habitat to find that it makes good sense. Rains, locally, may be rare in a dry grassland or semi-desert, but when they come they are commonly torrential. Pools formed may, in flat country, extend for a half mile or more although many will be smaller. All are likely to be shallow. A single pair of spadefoots produces several hundreds of zygotes, most of which develop into tadpoles. Further, there may be a hundred or more pairs successful in a single pool at the same time. As sunshine returns (especially if accompanied by high, dry winds, which are also common in xeric regions) evaporation begins and proceeds at a *very* fast rate. The pool shrinks rapidly and the tadpoles often become very crowded. Food tends to be scarce (though this varies greatly in different pools). Yet, if the animals are to continue their species, some must find food sufficient for their needs to reach metamorphosis before all water has gone. I know of no more efficient animals in finding food than spadefoot tadpoles in such places: organic matter of all sorts is utilized but there is still often not enough for all. This is the reason for the evolutionary development of social and other types of aggregational feeding, scooping and metamorphic aggregations and other habits peculiar to these tadpoles.

Now it is biologically more sound that some individuals be sacrificed than that *all* should die. If by cannibalism even a few succeed in reaching metamorphosis, they have a chance to produce

another generation of spadefoots. If all die, none of them can do so. Hence the development of cannibalism in western species (and in *Scaphiopus bombifrons* essentially first in the western, more xeric part of its range) is biologically sound. In this new development of cannibalism in tadpoles of *Spea* we are actually witnessing evolution of behaviour as well as morphology occurring.

Summary

This paper presents a summary of the evidence from the known habits of spadefoots as adults and as tadpoles, supplemented by the known geological and geographic changes in south-western North America since the late Mesozoic, that (1) *Scaphiopus* arose as a genus from pelobatid ancestors in south-western North America, as proposed by Tanner; (2) this occurred very early in the Cenozoic area; (3) special habits in breeding behaviour arose early and became fixed in the genotype before much migration from the area of origin occurred; (4) these changes were the result of intensive selection-pressure as the climate changed; (5) special developments in behaviour of the spadefoot larvae that adjusted them to life in the temporary pools occurred; and (6) new habits of food getting (including dimorphism with predaceous cannibalism) in tadpoles of the western group (*Spea*) are still developing.

Practically all of the facts upon which this conception rests have already been published, but this paper is the first attempt at a synthesis of these facts to form a whole picture of the importance of habits in evolutionary studies of spadefoots. As such, it is hoped that others may find stimulation to emphasize habits and their evolution in further studies to supplement the excellent researches in population genetics and in morphology which many now have in progress.

Acknowledgments

I am indebted to Dr. Harry Hoy and Dr. Harley P. Brown, Departments of Geography and Zoology respectively, University of Oklahoma, and to my wife, Mary G. Bragg, and William N. Bragg for critically reading the manuscript. Some of my geological ideas were clarified by an informal discussion with Dr. George G. Huffman, Department of Geology, University of Oklahoma. I here express appreciation for their aid.

REFERENCES

Abbot, C. C. (1884). Recent studies of the spadefoot toad. *Amer. Nat.*, **18,** 1075-1080.

Auffenberg, W. (1956). Remarks on some Miocene anurans from Florida with a description of a new species of Hyla. *Mus. comp. Zool.*, Breviara **(52),** 1-11.

Bader, Robert S. (1958). Similarity and recency of common ancestry. *Sys. Zool.*, **7,** 184-187.

Ball, Stanley C. (1936). The distribution and behviour of the spadefoot toad in Connecticut. *Trans. Conn. Acad. Arts and Sci.*, **32,** 351-379.

Bragg, Arthur N. (1940). Observations on the ecology and natural history of Anura. I. habits, Habitat and breeding of *Bufo cognatus Say. Amer. Nat.*, **74,** 322-349 and 424-438.

Bragg, Arthur N. (1941). Observations on the ecology and natural history of Anura, VIII. Some factors in the iniation of breeding behavior. *Turtox News*, **19,** 10-12.

Bragg, Arthur N. (1941a). Tadpoles of *Scaphiopus bombifrons* and *Scaphiopus hammondii. Wasmann Collector*, **4,** 92-94.

Bragg, Arthur N. (1943). Observations on the ecology and natural history of Anura. XVI. Life-history of *Pseudacris clarkii* (Baird) in Oklahoma. *Wasmann Collector*, **5,** 129-140.

Bragg, Arthur N. (1943a). Observations on the ecology and natural history of Anura. XV. The hylids and microhylids in Oklahoma. *Great Basin Nat.*, **4,** 62-89.

Bragg, Arthur N. (1944-45). Observations on the ecology and natural history of Anura. XII. The spadefoot toads in Oklahoma with a summary of our knowledge of the group. *Amer. Nat.*, **78,** 417-533 and (continued) **79,** 52-72.

Bragg, Arthur N. (1946). Some salientian adaptations. *Great Basin Nat.*, **7,** 11-15.

Bragg, Arthur N. (1946a). Aggregation with cannibalism in tadpoles of *Scaphiopus bombifrons* Cope, with some general remarks on the probable evolutionary significance of such phenomena. *Herpetologica*, **3,** 89-97.

Bragg, Arthur N. (1948). Additional instances of social aggregation in tadpoles. *Wasmann Collector*, **7,** 65-79.

Bragg, Arthur N. (1950). Some adaptations of survival value in spadefoot toads. Researches on the Amphibia of Okla. *Art.*, **7,** 101-116. Univ. of Okla. Press, Norman.

Bragg, Arthur N. (1950a). Observations on Scaphiopus, 1949 (Salientia: Scaphiopodidae). *Wasmann J. Biol.*, **8,** 221-225.

Bragg, Arthur N. (1951). Mass movements at metamorphis in the Savannah spadefoot *Scaphiopus hurterii* Strecker. *Proc. Okla. Acad. Sci* , **31,** 26-27.

Bragg, Arthur N. (1956). The amphibians of Greer County, Oklahoma. *Great Basin Nat.*, **15,** 27-31.

Bragg, Arthur N. (1956a). Further observations on spadefoot toads. *Herpetologica*, **12,** 201-204.

Bragg, Arthur N. (1957). Dimorphism and cannibalism in tadpoles of *Scaphiopus bombifrons* (Amphibia, Salientia). *Southwestern Nat.*, **1,** 105-108.

Bragg, Arthur N. (1959). Behavior of tadpoles of Hurter's spadefoot during an exceptionally rainy season. *Wasmann J. Biol.*, **17,** 23-42.

Bragg, Arthur N. (1960). Experimental observations on feeding of spadefoot tadpoles. *Southwestern Nat.*, **5**, 201-207.

Bragg, Arthur N. & Bragg, Wm. N. (1959). Variations in the mouth parts in tadpoles of *Scaphiopus* (Spea) *bombifrons* Cope, (Amphibia: Salientia). *Southwestern Nat.*, **3**, 55-69.

Bragg, Arthur N. & King, Otis M. (1960). Aggregational and associated behavior in tadpoles of the Plains Spadefoot. *Wasmann J. Biol.*, **18**, 273-289.

Bragg, Arthur N. & Smith, Charles C. (1948). Observations on the ecology and Natural history of Anura IX. Notes on breeding behavior in Oklahoma. *Great Basin Nat.*, **3**, 33-50.

Brattstrom, Bayard H. (1957). The phylogeny of the Salientia based on skeletal morphology. *Syst. Zool.*, **6**, 70-74.

Brown, Bryce C. (1950). An annotated check list of the reptiles and amphibians of Texas. XII + 259 pp. Baylor Univ. Press, Waco, Texas.

Clements, Fredric & Shelford, Victor E. (1939). *Bio-ecology*. III + 425 pp. New York: John Wiley & Sons.

Conant, Roger (1959). *A field guide to reptiles and amphibians of the United States and Canada east of the 100th meridian*. XVIII + 366 pp. Boston, Mass.: Houghton Mifflin Co.

Gilmore, R. J. (1924). Notes on the life history and feeding habits of the spadefoot toad of the western plains. *Colorado College Publ. Sci. Serv.*, **13**, 1-12.

Goin, Olive Brown (1955). *The world outside my door*. XII + 184 pp. New York: The McMillan Co.

Hansen, Keith L. (1958). Breeding patterns of the eastern spadefoot toad. *Herpetologica*, **14**, 57-67.

Hansen, Keith L. (1959). A study of *in vitro* ovulation in the eastern spadefoot, *Scaphiopus h. holbrooki*. *Quart. J. Fla. Acad. Sci.*, **22** (1), 1-13.

Hesse, Richard, Allee, W. C. & Schmidt, Karl P. (1937). *Ecological animal geography*. XIV + 597 pp. New York: John Wiley & Sons.

Holman, J. Allen (1958). The Pleistocene hepetofauna of Sabre-tooth Cave, Flodia. *Copeia* 1958 (4), 276-280.

King, Otis M. (1960). Notes on Oklahoma toads. *Southwestern Nat.*, **5**, 102-103.

Lindsdale, Jean S. (1938). Environmental responses of vertebrates in the Great Basin. *Amer. Midl. Nat.*, **19**, 1-206.

Miller, W. J. (1922). *Introduction to historical geology*. New York: D. Van Nostrand Co.

Neill, Wilfred T. (1957). Notes on metaporphis and breeding aggregations of the eastern spadefoot, *Scaphiopus holbrooki* (Harlan). *Herpetologica*, **13**, 185-187.

Noble, G. K. (1954). *The biology of the Amphibia*. Reprint of edition of 1931. New York: Dover Publ.

Orton, Grace (1954). Dimorphism in larval mouth parts in spadefoot toads of the *Scaphiopus hammondi* group. *Copeia*, 1954 (2), 97-100.

Pearson, Paul K. (1955). Population ecology of the spadefoot toad, *Scaphiopus h. holbrooki* (Harlan). *Ecol. Morph.*, **25**, 233-267.

Richmond, Neil D. (1947). Life history of *Scaphiopus holbrooki holbrooki* (Harlan). Part I. Larval development and behavior. *Ecology*, **28**, 53-67.

Romer, Alfred S. (1941). *Man and the vertebrates*. Univ. of Chicago Press.

Savage, R. Maxwell (1942). On the burrowing and emergence of the spadefoot toad. *Proc. Zool. Soc. Lond.*, **112**, 21-25.

Schucherit, Chas. (1915). *Historical Geology*. New York: John Wiley & Sons, Inc.

Stebbins, Robert C. (1951). *Amphibians of western North America*. Univ. of Calif. Press, Berkley and Los Angeles.

Storer, T. I. (1925). A synopsis of the Amphibia of California. *Univ. Calif. Publ. Zool.*, **27**, 1-342.

Tanner, Vasco M. (1939). A study of the genus Scaphiopus: The spadefoot toads. *Great Basin Nat.*, **1**, 3-26.

Trowbridge, Albert H. & Trowbridge, Minnie S. (1937). Notes on the cleavage rate of *Scaphiopus bombifrons* Cope with additional remarks on certain aspects of its life history. *Amer. Nat.*, **71**, 460-480.

Turner, Frederick B. (1952). The mouth parts of tadpoles of the spadefoot toad, *Scaphiopus hammondi*. *Copeia*, 1952 (3), 172-175.

Wasserman, Aaron O. (1957). Hybridization in three species of spadefoot toads. *Copeia*, 1957 (2), 144-145.

Wright, Albert H. (1929). Synopsis and description of North American Tadpoles. *Proc. U.S. Nat., Mus.*, **74** (Art. II), 1-70.

Accepted for publication 27*th February*, 1961.

THE EFFECT OF DIURNAL CHANGES IN TEMPERATURE, DISSOLVED OXYGEN AND ILLUMINATION ON THE BEHAVIOUR OF ROACH (*Rutilus rutilus* (L.)), BREAM (*Abramis brama* (L.)) AND PERCH (*Perca fluviatilis* (L.))

By J. S. ALABASTER

Ministry of Agriculture, Fisheries and Food, London

AND K. G. ROBERTSON

Water Pollution Research Laboratory, Stevenage

Introduction

Temperature, dissolved oxygen and other factors in the freshwater habitat in Britain are subject not only to gradual seasonal changes but also to more rapid diurnal fluctuations, particularly during the summer when there is the greatest amount of solar radiation and aquatic plant growth. Maximum values of temperature and dissolved oxygen are reached during the afternoon and minimum values at about dawn (Butcher, Pentelow & Woodley, 1928). Diurnal changes have been observed in the behaviour of fish both in the field and in the laboratory; for example, Crossman (1959) has recorded diurnal movements of shiners, Swift (private communication) has been making extensive continuous observations of the activity of trout in cages in Windermere Dudek (1957) has described diurnal changes in the feeding of silver bream (*Blicca bjoerkna*) and Jones (1956) found that the minnow (*Phoxinus phoxinus*) in the laboratory, when provided with shelter, was most active at sunrise and at sunset. Other relevant references are given by Breder (1959) and there is also the testimony of anglers that fish are more easily caught at particular times of day.

In some species the diurnal pattern of behaviour has been attributed to changes in temperature (Maruyama, 1958) and in others it appears to have been caused by change in illumination (Jones, 1956; Dudek, 1957) but there is the further possibility that the existing diurnal variations in concentration of dissolved oxygen or in other chemical factors or in the behaviour of food organisms may also be important. Apart from the literature already cited there appear to be few published accounts of observations or of experimental work on British species. During the summer of 1959 an opportunity was taken to observe the behaviour of coarse fish throughout 24-hour periods in a large outdoor tank. At the same time, measurements of natural changes in temperature and dissolved oxygen were made and some experiments were carried out in which temperature and dissolved oxygen were changed during the day or prevented from changing during the night.

Materials and Methods

The tank used for these observations and experiments is about 110 ft. long, 21 ft. wide and 4 ft. deep. It was subdivided by vertical partitions about 16 ft. long extending from alternate sides across the tank to form a winding channel about 4 ft. wide and 500 ft. long and having 26 convolutions (or bays). Pumps and pipe lines were arranged to withdraw water from any point in the channel, convey it to a well and recirculate it anywhere. In the well the water temperature could be raised by injecting steam (supplied from the Grove Road Generating Station) and the water could be either aerated with oxygen to prevent the dissolved oxygen concentration falling overnight or deoxygenated by treating it with sodium sulphite plus cobalt nitrate as a catalyst. In the presence of the cobalt catalyst the sulphite combines very quickly with the oxygen dissolved in the water to form sulphate so that as the concentration of dissolved oxygen is reduced the concentration of sulphate increases. Although the behaviour of fish may be affected by chemicals (Breder, 1959) a control experiment with roach in the channel showed that increasing the concentration of sodium sulphate to 100 p.p.m., which is considerably in excess of that produced by the deoxygenation technique, had no visible effect on behaviour.

The tank was partly filled with mains water supplied by the Metropolitan Water Board several months before observations were started during which time it acquired a growth of algae and accumulated a $\frac{1}{4}$ inch thick layer of decaying organic matter and dirt from the atmosphere. During the period of the experiments the depth

was kept at about 8 inches by the addition of fresh water when necessary.

The fish used for the experiments were obtained during the winter from the Metropolitan Water Board aqueduct near Staines. They were all about 20 cm. long and were kept together at seasonal temperature in stock tanks of 40 to 100 gallons capacity, and fed on raw minced heart and biscuit. Each species was used separately. A group of 10 or more individuals was used at a time because they are all shoaling fish whose normal physiology and behaviour might have been different if single fish were tested (Breder, 1959). There was a further advantage in using several fish since they generally formed into one shoal and so were much easier to locate and observe than single fish. They were observed at regular, usually ¼-hour intervals, unless they were moving around a great deal when they were watched almost continuously. A record was kept not of total activity of individual fish but simply of the resultant movement of the shoal or shoals. When it was dark the fish were found with the aid of a hand torch taking a 0·9 watt bulb, which did not seem to disturb them. Water temperatures were recorded continuously by mercury-in-steel recording thermometers which were placed near a shoal when it had settled down and also by remote reading resistance thermometers at various points in the channel. Water samples were taken usually at hourly intervals at a point within 20 feet of the fish and the dissolved oxygen concentration determined by the Winkler method (Alsterberg, 1925). No measurements were made of light intensity but in examining the results the official time of sunset and sunrise was used.

Results

(a) Overnight Observations in Natural Conditions

The first overnight observations were made on a group of 15 roach which when observed in the channel for the previous 2 weeks between 9 a.m. and 5 p.m. were seen only at the end of Bays 2 and 3. Observations overnight (Fig. 1a) showed that they remained in these bays until just after dawn when they became much more active and swam over a considerable length of the channel. At this time both the temperature and the dissolved oxygen reached their minimum values, the temperature having fallen by 4°C. from 22 to 18°C. and the dissolved oxygen concentration having fallen by 3 parts per million from 10·5 to 7·5 p.p.m.

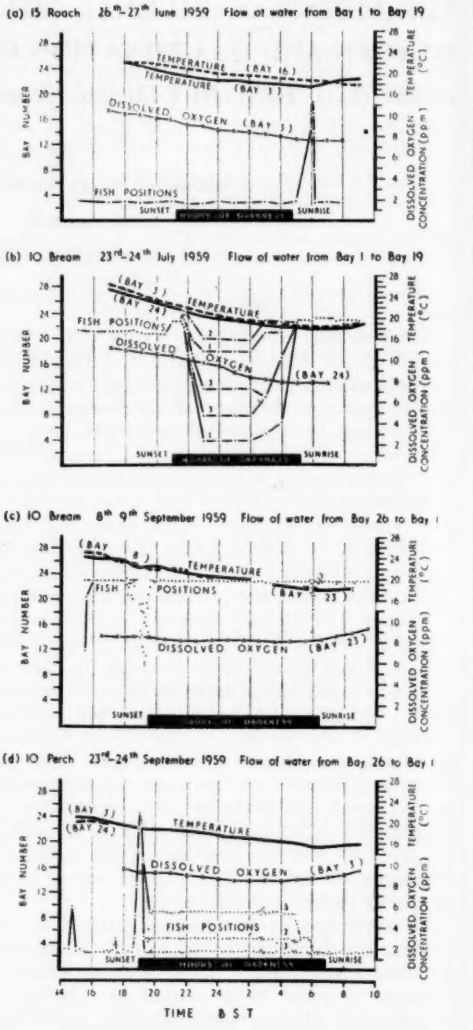


Fig. 1. Overnight observations of fish positions and natural changes in temperature and dissolved oxygen in a winding channel. When the fish are not in one shoal the distribution between groups is indicated.

Similar observations were made with bream and perch and a period of increased activity found not only at dawn but at dusk too. The results obtained on two occasions with bream are shown in Fig. 1b and 1c. in the first of which the shoal is seen to split up into smaller groups at dusk. Division of the shoal into small units,

sometimes comprising a single fish, was also observed in the evening with perch (Fig. 1d), but with both species the fish came together again at dawn forming a single shoal which remained intact throughout the day.

(b) Experimental Work

Other work (Alabaster, in preparation) has shown that a rapid fall in temperature is associated with increased activity among shoals of roach and bream; in one experiment (shown in Fig. 2) with roach of the same size as those used in the overnight observations illustrated in Fig. 1a, there was a marked increase in activity during the daytime with a drop of 2°C. in half an hour. This suggests that the early morning activity which had been seen could have been

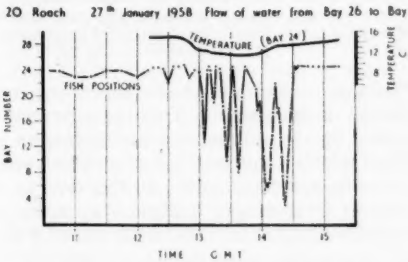

20 Roach 27th January 1958 Flow of water from Bay 26 to Bay 1
TEMPERATURE (BAY 24)
FISH POSITIONS
BAY NUMBER
TEMPERATURE °C
TIME G M T

Fig. 2. Effect of a fall in temperature during the daytime on the movement of a shoal of roach in a winding channel.

caused by the fall in temperature at that time. To test this hypothesis overnight observations were repeated on two occasions when cooling of the water in the channel during the early morning was prevented by the use of steam heating, though the dissolved oxygen concentration was allowed to fall naturally. The results of these observations are shown in Fig. 3a and 3b. There was again no movement of the shoal during most of the night and still a noticeable movement at dawn; in the second of these experiments there was also some increase in activity in the afternoon and evening as well. This suggests that the fall in temperature is not necessarily responsible for diurnal activity in these species though if a fall in temperature occurs during the daytime it can produce a reaction similar to that seen at dawn.

In another experiment designed to test whether the behaviour of the fish could be affected by a fall in dissolved oxygen concentration, the temperature was maintained at a constant high value and the dissolved oxygen concentration was

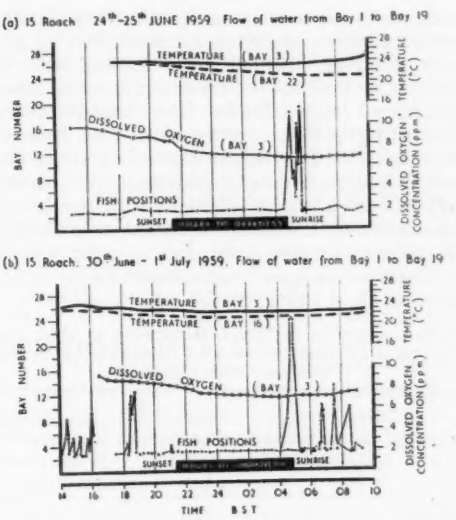

(a) 15 Roach 24th–25th JUNE 1959 Flow of water from Bay 1 to Bay 19
TEMPERATURE (BAY 3)
TEMPERATURE (BAY 22)
DISSOLVED OXYGEN (BAY 3)
FISH POSITIONS
SUNSET
SUNRISE
BAY NUMBER
DISSOLVED OXYGEN CONCENTRATION (ppm)
TEMPERATURE (°C)
(b) 15 Roach. 30th June – 1st July 1959. Flow of water from Bay 1 to Bay 19
TEMPERATURE (BAY 3)
TEMPERATURE (BAY 16)
DISSOLVED OXYGEN (BAY 3)
FISH POSITIONS
SUNSET
SUNRISE
TIME B S T

Fig. 3. Overnight observations of roach shoal movement in a winding channel when temperature is kept constant and dissolved oxygen concentration falls naturally during the night.

reduced during the day by the controlled addition of sodium sulphite and cobalt nitrate. The results (Fig. 4a) show that there was a marked

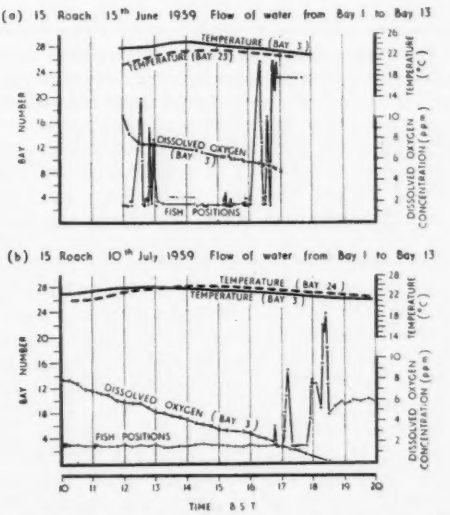

(a) 15 Roach 15th June 1959 Flow of water from Bay 1 to Bay 13
TEMPERATURE (BAY 3)
TEMPERATURE (BAY 23)
DISSOLVED OXYGEN (BAY 3)
FISH POSITIONS
(b) 15 Roach 10th July 1959 Flow of water from Bay 1 to Bay 13
TEMPERATURE (BAY 24)
TEMPERATURE (BAY 3)
DISSOLVED OXYGEN (BAY 3)
FISH POSITIONS
BAY NUMBER
DISSOLVED OXYGEN CONCENTRATION (ppm)
TEMPERATURE (°C)
TIME B S T

Fig. 4. Effect of a fall in dissolved oxygen concentration during the daytime on the movement of a shoal of roach in a winding channel.

increase in the activity of the fish when the dissolved oxygen concentration had fallen by just over 2 p.p.m. followed by a second burst of activity by the time the concentration had fallen a further 2 p.p.m. The fish then ranged over the whole length of the channel and settled down in the region of the highest concentration of dissolved oxygen. Similar experiments were carried out with roach (Fig. 4b) and with perch and bream and the results are summarized in Table I. They show that even comparatively slow changes in dissolved oxygen concentration cause movement in these three species.

Table I. Dissolved Oxygen Concentration at which Fish Exposed to a Falling Concentration Move and Occupy New Positions in the Channel.

Species	Rate of fall in concentration (p.p.m./hour)	Initial concentration (p.p.m.)	Concentration when fish moved away (p.p.m.)
Roach	3·7	10·1	7·6
	0·6	7·6	5·6
	0·9	7·5	1·6
	0·9	8·0	1·0
Bream	1·5	8·8	1·0
	2·4	12·5	1·5
Perch	1·5	11·1	6·7
	1·5	11·1	2·3
	1·8	11·2	3·0
	1·8	11·2	1·9

It appears from the above results that either a fall in temperature or a fall in dissolved oxygen concentration at dawn could have caused the increase in activity which was observed at this time, although other stimuli cannot be excluded. To eliminate the effect of temperature and dissolved oxygen changes, roach were observed when provision was made throughout the night not only to prevent the temperature in the tank from falling but also to maintain the dissolved oxygen concentration at a high value by bubbling oxygen into the well. Because ambient temperatures during the day were higher than expected, water temperature was not stabilized at the required value (23°C.) until about midnight but thereafter both temperature and dissolved oxygen concentration remained constant. The results (Fig. 5) show that there was very limited activity of the fish during the night but pronounced activity about dawn, and suggest that the natural fall in temperature and in dissolved oxygen concentration are not the main stimuli of activity at this time.

There is some evidence in Fig. 3b and Fig. 5 of increased activity of fish in the evening but this is much less consistent than that for dawn activity, particularly in Fig. 5, which shows a rapid increase in temperature of 4 or 5°C. during

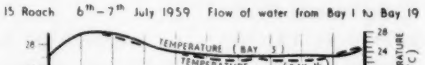


Fig. 5. Overnight observations of roach shoal movement in a winding channel when temperature and dissolved oxygen concentration are artificially kept constant at dawn.

the afternoon which may have caused the burst of activity in the evening. This interpretation is supported by the results of experiments, an example of which is given in Fig. 6 in which roach which were subjected early in the day to an increase in temperature became very active by the time the temperature had been raised 4°C.

Discussion

Diurnal variation in behaviour has been observed in the three species investigated; increased activity was invariably shown at dawn by all species and also at dusk by bream and perch, but only on some (two in four) occasions by roach. A similar increase in activity can be caused experimentally by change in temperature or by change in dissolved oxygen concentration. Since changes in these two factors often occur at dawn and dusk they may account to some extent for the increased activity which has been observed at these times, but when (as in the experiment with roach shown in Fig. 5) the temperature and the dissolved oxygen concentration were kept constant overnight, dawn activity still occurred. Moreover when observations on diurnal variation in behaviour were made on bream and perch in September there was little natural variation in temperature or dissolved oxygen. It appears therefore that at least three factors may be involved, temperature, dissolved oxygen and illumination. From the experiments reported here diurnal light seems of primary importance but its effect may have been reinforced by changes in temperature and dis-

solved oxygen. Jones (1956) found that light influenced the diurnal pattern of behaviour of the minnow, Dudek (1958) found the same for the feeding of bream, and Maruyama's (1958) data suggest that movement of *Tilapia* was initiated at dusk irrespective of temperature.

Breaking up of shoals was observed only with bream and perch and only in the evening. As this type of behaviour is commonly caused in shoaling fish (Breder 1959), by the reduction of the light intensity to a value at which individuals in a shoal cannot maintain visual contact with each other, it seems likely that this explanation could account for the division of the shoals of bream and perch seen in these experiments. It is interesting to note that when the temperature or dissolved oxygen concentration was changed during the day the shoals tended to remain intact.

In the experiments in which fish were exposed to changing temperature or dissolved oxygen concentration they not only became more active and increased their range of swimming but also tended, if a choice was available, to move away from regions where conditions were changing and to settle down where conditions were nearer those to which they were acclimatized before the experiments started. Thus when exposed to a rise in temperature they would apparently select a lower one if available and if exposed to a fall in dissolved oxygen concentration would come to rest in water at a higher value. High extremes of temperature and low extremes of dissolved oxygen concentration are of course lethal but the changes which caused fish to move away are smaller than those which would kill them rapidly, even if they were suddenly exposed to them (Alabaster, in preparation). Thus, in the experiment shown in Fig. 6 the temperature at which roach moved away (29° to 30°C.) is lower than

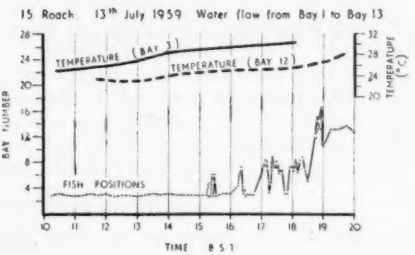


Fig. 6. Effect of a rise in temperature during the daytime on the movement of a shoal of roach in a winding channel.

that (approx. 31·5°C.) which would allow them to live at least 24 hours (Cocking, 1959a). Only some of the information about lethal concentrations of dissolved oxygen can be used for comparison with concentrations causing increased activity because of differences in temperature in the two sets of experiments but the lowest concentration to which the dissolved oxygen fell before perch moved away was 1.9 p.p.m. (see Table I) which is higher than the values found lethal by Downing & Merkens (1957) and Alabaster, Herbert & Hemens (1957). The corresponding concentration for roach was 1·0 p.p.m. (at 24°C.) whereas the concentration at which roach died when kept in sealed bottles (at 30°C.) is 0·82 p.p.m. (Cocking, 1959b). Although the lowest concentration of dissolved oxygen at which roach showed activity and moved away was on the borderline of lethality, the majority of concentrations for roach and perch were clearly not lethal.

The effect of change in temperature and dissolved oxygen on fish behaviour is of further interest because the increase in activity and subsequent apparent selection of available conditions could have considerable survival value if it took place in rivers in which there are large and fairly rapid fluctuations in temperature such as are caused by the discharge of heated condenser water from power generating stations operating at peak load times only (Gameson, Gibbs & Barrett, 1959) and when there are fluctuations in dissolved oxygen caused by the discharge of oxidizable effluents such as sewage (Allan, Herbert & Alabaster, 1958).

A potential survival value of such behaviour is suggested by these experiments for though conditions in the tank have been very different from those in rivers it has been possible to demonstrate a selection of conditions on a larger scale than in most laboratory studies (Jones, 1952). Behaviour may differ under natural conditions but a comparison of the effect in the field and in artificial experiments of diurnal phenomena on fish behaviour cannot yet be made, because of the difficulty in making observations in natural conditions: on the other hand, there is some evidence that fish do in some circumstances successfully avoid lethal high temperatures in rivers receiving heated effluents (Alabaster, in preparation) and also avoid regions of low concentrations of dissolved oxygen in rivers polluted by sewage effluent (Alabaster, 1959).

Summary

1. Increased activity at dawn and dusk has been observed in roach, bream and perch and breaking up of shoals at night has occurred in perch and bream.

2. Roach became active at dawn even when the temperature and dissolved oxygen concentration were kept fairly constant. This suggests that another factor, probably diurnal change in light, stimulates the fish.

3. Non-lethal changes in temperature and dissolved oxygen concentration cause fish to become more active irrespective of light. This reaction is considered to have survival value for fish in rivers polluted by heated and oxidizable effluents.

Acknowledgments

The experimental tank and laboratory facilities were kindly provided by the Central Electricity Generating Board at their Biological Laboratories at Grove Road, St. John's Wood, and services including the supply of steam were kindly supplied by the Grove Road Generating Station. The authors are grateful to the Metropolitan Water Board for permission to collect fish from their waters and they also wish to acknowledge the assistance given by their colleague Mr. R. J. B. Davies in carrying out the experiments.

This paper is published by permission of the Ministry of Agriculture, Fisheries and Food and the Department of Scientific and Industrial Research.

REFERENCES

Alabaster, J. S. (1959). The distribution of dissolved oxygen and fish in a sewage effluent. *J. anim. Ecol.*, **28**, 283-291.

Alabaster, J. S., Herbert, D. W. M. & Hemens, J. (1957). The survival of rainbow trout (*Salmo gairdnerii* Richardson) and perch (*Perca fluviatilis* L.) at various concentrations of dissolved oxygen and carbon dioxide. *Ann. appl. Biol.*, **45** (1), 177-188.

Allan, I. R. H., Herbert, D. W. M. & Alabaster, J. S. (1958). A field and laboratory study of fish in a sewage effluent. Fishery Investigation Series I, VI(2), 1-76. H.M.S.O.

Alsterberg, G. (1925). Methoden zur Bestimmung von im Wasser gelösten elementaren Sauerstoff bei Gegenwart von salpetriger Säure. *Biochem. Z.*, **159**, 36.

Breder, C. M. (1959). Studies on social groupings in fishes. *Bull. Amer. Mus. nat. Hist.*, **117**, Article 6. New York.

Butcher, R. W., Pentelow, F. T. K. & Woodley, J. W. A. (1928). The diurnal variation of the gaseous constituents of river waters, Part IV. *Biochem. J.*, **22** (6), 1478-1489.

Cocking, A. W. (1959a). The effects of high temperature on Roach (*Rutilus rutilus*). I. The effects of constant high temperatures. *J. exp. Biol.*, **36** (1), 203-216.

Cocking, A. W. (1959b). The effects of high temperatures on Roach (*Rutilus rutilus*). II. The effects of temperature increasing at a known constant rate. *J. exp. Biol.*, **36** (1), 217-226.

Crossman, E. J. (1959). Distribution and movements of a predator, the rainbow trout, and its prey the red shiner in Paul Lake, British Colombia. *J. Fish. Res. Bd. Canad.*, **16** (3), 247-267.

Downing, K. M. & Merkens, J. C. (1957). The influence of temperature on the survival of several species of fish in low tensions of dissolved oxygen. *Ann. appl. Biol.*, **45** (2), 261-267.

Dudek, J. (1957). Príspevok k určeniu vplyvu svetla na intenzitu prijímania potravy u piesta zelenkavého (*Blicca bjoerkna* L.). (Contribution to the determination of the influence of light on the intensity of the uptake of food by *Blicca bjoerkna* L.). *Biologia*, **12**, 5, 374-76. Bratislava.

Gameson, A. L. H., Gibbs, J. W. & Barrett, M. J. (1959). A preliminary temperature survey of a heated river. *Wat. & Wat. Engng.*, **63**, 13-17.

Jones, F. R. H. (1956). The behaviour of minnows in relation to light intensity. *J. exp. Biol.*, **33** (2), 271-281.

Jones, J. R. E. (1952). The reactions of fish to water of low oxygen concentration. *J. exp. Biol.*, **29** (3), 403-415.

Maruyama, T. (1958). An observation on *Tilapia mossambica* in pond referring to the diurnal movement with temperature change. *Bull. freshw. Fish. Res. Lab.*, Tokyo (8) 25-32.

Accepted for publication 1st January, 1961.

THE STIMULI RELEASING THE STINGING RESPONSE OF HONEYBEES

By J. B. FREE

Rothamsted Experimental Station, Harpenden, Herts.

Introduction

Beekeepers believe that dark coloured clothes, strange scents, and jerky movements provoke honeybees to sting them (see Morse & Ghent, 1959). The present experiments investigate the effect of these and other factors on releasing stinging and ways to decrease it.

Method

Cotton wool was wrapped in muslin to make balls approximately an inch in diameter, which were suspended from thread and jerked in front of hive entrances or just above hives open at the top. Bees which stung left their stings, which have backward-sloping barbs, embedded in the balls.

No attempt was made to avoid handling the balls, except after odours had been deliberately added to them, so they all had some human odour.

Results

Effect of Colour

The muslin coverings of the balls were white, black, blue or yellow. Two colours were compared at a time; 8 balls of each colour were arranged in a 4 × 4 latin square, and suspended by 2 inch threads from a 2 foot square hardboard background. The hardboard was covered with muslin dyed with one of the colours being tested. The balls were jerked over hives open at the top until they had been stung sufficiently for a comparison to be made. Five tests were made with each colour background (Table I).

In every test black balls were stung more than white, and blue more than yellow, particularly when the background contrasted with the black or blue balls. White balls were stung more than yellow in 4 of the 5 tests with the yellow background, and yellow balls stung more than white in 4 out of 5 tests with the white background.

Effect of Previous Stings

Eight newly stung balls (mean of 4·6 stings per ball) were arranged in a 4 × 4 latin square with 8 fresh balls of the same colour. In 6 of 9 trials the balls with stings already embedded in them were stung more than the controls (Table II).

Table I. Effect of Colour in Causing Stinging.

Mean no. stings per test in balls of different colours			
White background		Black background	
White balls	Black balls	White balls	Black balls
6·8	36·6	24·8	38·0
Yellow background		Blue blackground	
Yellow balls	Blue balls	Yellow balls	Blue balls
16·2	44·6	15·0	26·4
Yellow background		White background	
Yellow balls	White balls	Yellow balls	White balls
22·8	33·8	40·2	22·2

Table II. Effect of Previous Stings.

	No. times stung	
	Balls with stings already present	Fresh balls
Trial 1	27	33
„ 2	9	9
„ 3	33	21
„ 4	33	15
„ 5	4	6
„ 6	21	16
„ 7	20	19
„ 8	33	15
„ 9	70	10
Mean	27·8	16·0

To overcome the possibility that nearness of the balls to each other influenced the result, further tests were made in which 2 balls were suspended 18 inches apart on the horizontal bar of a T-shaped wooden support and jerked in front of a hive entrance. One of the balls (experimental) had previously been stung (a mean of 5·6

times) and the other (control) had not; the positions of the 2 types were interchanged after each test. The results were as follows:

Balls containing stings stung more:	18 trials
Control balls stung more:	1 trial
Both balls stung equally:	4 trials
Mean no. additional stings in experimental balls:	2·3
Mean no. stings in control balls:	0·7

In all later tests only 2 balls were presented together and attempts were made to stop a test when only one of them had been stung.

The previously stung balls were probably stung more because of an odour associated with the stings, but they may also have acquired the smell of some other substance the stinging bees perhaps secreted through their mouth-parts. To find whether the sting smell alone was sufficient, the abdomens of 2 recently decapitated bees were pushed against each experimental ball until they stung it, and these balls were then compared with unstung controls. The results were:

Balls containing stings stung more:	19 trials
Control balls stung more:	2 trials
Both balls stung equally:	4 trials
Mean no. additional stings in experimental balls:	4.0
Mean no. stings in control balls:	1·7

Effect of Smoke

The experimental balls had smoke from burning cardboard in a beekeeper's smoker blown over them for 30 seconds immediately before a trial. In 11 trials they were stung more than the controls, in 8 trials less, and in one trial as much (no significant difference). Similar trials were then made in which the experimental and control balls had recently received equal numbers of stings. The results were:

Experimental balls stung more:		5 trials
Control balls stung more:		15 trials
Both balls stung equally:		0 trials
Mean no. additional stings in	experimental balls:	0·90
	control balls:	1·65

Thus, although the smoke was not repellant, it decreased the stinging of previously stung balls ($P<0.05$), presumably by masking the sting odour.

Effect of Colony Odour

Balls were kept in double-walled, wire-gauze cages between the combs of a colony for 24 hours in an attempt to impart the colony odour to them. They were then without further handling compared with clean balls. When presented to the colony in which they had been kept, the experimental balls were stung more times than the controls in 15 trials and fewer in 10 trials (no significant difference). When presented to another colony the experimental balls were stung more in 13 trials, the control balls more in 11 trials, and both were stung equally in one trial.

Balls were kept 24 hours in 2 colonies (A & B). One ball from each was presented to colony A and colony B on alternate trials. Bees of colony A stung balls kept in colony A more in 12 trials, balls kept in colony B more in 3 trials, and both balls equally in one trial. Bees from colony B stung balls kept in colony B more in 13 trials, and balls kept in colony A more in 2 trials. Therefore bees stung balls which had been in their own colony more than they stung balls from the other colony ($P<0.001$).

Effect of Animal Scent

Balls were put in small glass dishes with voles or shrews for 1-3 hours before being presented to a colony, together with a clean control ball. The results were:

		Experimental balls kept with Voles	Shrews
Experimental balls stung more:		19 trials	24 trials
Control balls stung more:		5 ,,	1 ,,
Both balls stung equally:		1 ,,	0 ,,
Mean no. stings in	experimental balls:	2·24	4·00
	control balls:	1·00	0·40

When the experimental balls had human sweat (from the forehead) rubbed on them and control balls a few drops of distilled water the results were:

Experimental balls stung more:		21 trials
Control balls stung more:		2 ,,
Both balls stung equally:		2 ,,
Mean no. stings in	experimental balls	3·64
	control balls	0·64

Effect of Repellants

Six drops of a possible repellent (i.e. dimethylphthalate, citronellol, methylsalicylate) were put on each experimental ball and 6 drops of distilled water on each control ball. Table III shows that the repellents decreased the frequency of stinging.

Both experimental and control balls were kept with voles for 3 hours before drops of dimethylphthalate were put on the experimental balls and distilled water on the control balls. The results were:

Experimental balls stung more:		0 trials
Control balls stung more:		24 trials
Both balls stung equally:		1 trial
Mean no. stings in	experimental balls:	0·24
	control balls:	3·28

Table III. Effect of Repellents on Stinging.

Repellent	No. trials in which:			Mean no. of stings in:	
	Balls with repellent stung more	Control balls stung more	Balls stung equally	Balls with repellent	Control balls
Dimethylphthalate	10	70	0	0·76	3·20
Citronellol	1	19	1	0·45	2·00
Methylsalicylate	1	19	0	0·10	2·74

Effect of Texture

It is often supposed that bees are more inclined to sting rough than smooth textured clothing (see Morse & Ghent, 1959). In the first experiment balls of muslin covered with wool were tested against balls of wool covered with muslin. All balls were dyed black. In 6 trials the muslin-covered balls, and in one trial the wool-covered balls, were stung more, and in 3 trials both were stung equally. However, during presentation the wool-covered balls had at least as many bees clinging to them as the muslin-covered balls and it seemed possible that the wool covered balls tended to have fewer stings because the bees could withdraw their stings more readily from them.

In the next experiment all balls had wool inside and muslin outside, but one ball in each trial had strands of wool wound round it to cover a total of about half its surface area, leaving ample space between the strands for the bees to sting the muslin. The results were:

Balls covered with wool and muslin stung more: 17 trials
Balls covered with wool only stung more: 2 trials
Both balls stung equally: 1 trial
Mean no. strings in balls covered with { wool and muslin: 2·30 ; wool only: 0·45

Hence it seemed that the rougher texture of wool had more readily released stinging but possibly the odour of wool was also influential because although experimental and control balls contained wool, only the experimental balls had wool on the outside. However, when muslin-covered balls containing muslin and wool respectively were compared, the following results were obtained:

Balls containing muslin stung more: 17 trials
Balls containing wool stung more: 1 trial
Both balls stung equally: 2 trials
Mean no. stings in balls containing { muslin: 2·4 ; wool: 0·55

It is therefore unlikely that the smell of wool caused more stinging than that of muslin alone, although, because of the possibility that bee stings were more readily retained in balls made entirely with muslin, this has not been decisively shown.

Effect of Movement

One ball on a wire was held motionless 2 inches in front of a hive entrance. Another ball suspended from a cotton thread was jerked up and down about 6 inches further along the hive entrance. The results were:

Jerked balls stung more: 29 trials
Motionless balls stung more: 1 „
Both balls stung equally: 0 „
Mean no. stings in { jerked balls: 5·0 ; motionless balls: 0·3

Two balls were suspended by 3 inch threads from the ends of sticks and whirled in 6 inch circles at a hive entrance, one ball moving approximately twice as fast as the other. The results were:

Faster moving balls stung more: 29 trials
Slower moving balls stung more: 1 „
Both balls stung equally: 0 „
Mean no. stings in { faster moving balls: 2·7 ; slower moving balls: 0·2

Discussion and Conclusions

It is to be expected that the scent of mammals, many of which are natural enemies of honeybees, may encourage stinging and that once an object has been stung it is more likely to get further stings. Huber (1814) presented the sting of a bee at a hive entrance and found that it was attacked.

Honeybees of the same colony have the same distinctive odour (v. Frisch & Rosch, 1926; Kaltofen, 1951; Kalmus & Ribbands, 1952) which is distributed over their bodies (Free,

1956; Renner, 1960) and results, at least in part, from absorption of scents inside their hives (Renner, 1960) in much the same way as with bumblebees (Free 1958a). Common intruders of a honeybee colony are honeybees from other colonies which have either arrived inadvertently (Free, 1958b) or with intent to rob (e.g. Cale, 1949). When recognized by their strange odour they are sometimes attacked (Butler & Free, 1952; Ribbands, 1954). Presumably balls which were kept inside a honeybee colony acquired something of its odour but it is difficult to understand why bees attacked balls kept in their own colony more than those kept in another.

Because the visual acuity of an insect eye is small, objects are more readily perceived when moving. Dead or 'model' bees are attacked when jerked among small numbers of bees in cages (Lecomte, 1951) or at the hive entrance (Butler & Free, 1952), and the jerky flight of robber bees induces guard bees to attack them (Free, 1954). Therefore it is not surprising that rapidly moving balls received more stings.

To reduce stinging, beekeepers should wear clean, light-coloured, clothing of smooth texture, and they should avoid rapid movement and sweating. Smoking the site of a sting will help to prevent further stings. Probably repellents can further decrease stinging.

Summary

1. The factors inducing honeybees to sting were investigated by comparing the number of times cotton wool balls treated in different ways were stung.

2. Dark coloured balls were stung more than light coloured, particularly against dark backgrounds.

3. The odour of sting venom encouraged further stinging, but the effect was overcome by smoke. General bee odour did not encourage stinging and bees were more likely to sting balls with the odour of their own than of another colony.

4. Animal scent and the smell of human sweat encouraged stinging and various repellents discouraged it.

5. Bees probably sting materials of rough texture more readily than smooth.

6. Rapidly moving objects were stung more often than slowly moving ones.

REFERENCES

Butler, C. G. & Free, J. B. (1952). The behaviour of worker honeybees at the hive entrance. *Behaviour*, **4**, 262-292.

Cale, G. H. (1949). Common practices in management. Ch. 9 of *The Hive and the Honeybee*. Ed. R. A. Grout, Hamilton Ill.: Dadant.

Free, J. B. (1954). The behaviour of robber honeybees. *Behaviour*, **7**, 233-240.

Free, J. B. (1956). A study of the stimuli which release the food begging and offering responses of worker honeybees. *Brit. J. anim. Behav.*, **4**, 94-101.

Free, J. B. (1958a). The defence of bumblebee colonies. *Behaviour*, **12**, 233-242.

Free, J. B. (1958b). The drifting of honey-bees. *J. agric. Sci.*, **51**, 294-306.

Frisch, K. v. & Rosch, G. A. (1926). Neue Versuche uber die Bedeutung von Duftorgan und Pollenduft fur die Verstandigung im Bienenvolk. *Z. vergl. Physiol.*, **4**, 1-21.

Huber, F. (1814). Nouvelles observations sur les abeilles II. Transl. 1926. Hamilton, Ill.: *American Bee Journal*.

Kalmus, H. & Ribbands, C. R. (1952). The origin of the odours by which honeybees distinguish their companions. *Proc. roy. Soc. B.*, **140**, 50-59.

Kaltofen, R. S. (1951). Das Problem des Volksduftes bei der Honigbiene. *Z. vergl. Physiol.*, **33**, 462-475.

Lecomte, J. (1951). Récherches sur le compartement agressif des ouvrières *d'Apis Mellifica*. *Behaviour*, **4**, 60-66.

Morse, R. A. & Ghent, R. L. (1959). Protective measures against stinging insects. *New York Sta. J. Med.*, **59**, 1546-1548.

Renner, M. (1960). Das Duftorgan der Honigbiene und die Physiologische Bedeutung ihres Lockstoffes. *Z. vergl. Physiol.*, **43**, 411-468.

Ribbands, C. R. (1954). The defence of the honeybee community. *Proc. roy, Soc. B.*, **142**, 514-524.

Accepted for publication 24*th February*, 1961.

FACTORS INFLUENCING DISTRESS CALLING IN CHICKS, WITH SPECIAL REFERENCE TO TEMPERATURE CHANGES AND SOCIAL ISOLATION

By I. C. KAUFMAN and R. A. HINDE

Sub-Department of Animal Behaviour, Madingley, Cambridge

Introduction

Imprinting of the following response of nidifugous birds only occurs during a certain sensitive period, which in domestic chicks ordinarily extends up to approximately 3 days after hatching (Jaynes, 1957; Hess, 1959). At least four views about the factors determining the close of this sensitive period have been advanced:

(i) The sensitive period is limited by an internally determined waning of the tendency to follow (Lorenz, 1935; Fabricius, 1951).

(ii) The sensitive period is limited by the development of fear responses to strange objects, which inhibit positive social responses (Hinde, 1955; Hinde, Thorpe & Vince, 1956; Hess, 1956).

(iii) Although fear is an important factor in some cases, it cannot be the only factor limiting the sensitive period, for ducklings (Weidmann, 1956) and chicks (Jaynes, 1956) tested after the sensitive period is over neither follow the model nor show fear of it. Guiton (1959) found that socially reared chicks ceased to follow the model at a younger age than chicks reared in isolation, and thus concludes that socialization has an inhibitory effect on the following response to unfamiliar objects.

(iv) Moltz (1960) stresses the maturation of fear responses, but suggests that they act in a rather different way from that indicated in (ii). He suggests that, during the sensitive period, the moving object becomes associated with a low 'anxiety drive'. Henceforward the object has anxiety-reducing properties, and acts as a reinforcer. After the sensitive period the anxiety drive is no longer low, and these properties cannot be acquired.

The last three of these views emphasize either the formation of social bonds with brood mates or the elicitation of fear or anxiety. In the present study we have therefore attempted to clarify the extent to which 'distress calls' are induced by moving a chick from one pen to another at various ages, as happens in imprinting experiments, with particular reference to the roles of isolation from the brood mates and temperature changes. The calls given by young chicks fall into two groups—'distress' or 'lost peeping' calls which are elicited by isolation from companions, cold, hunger, thirst, pain, restraint or approach of a large object, and 'pleasure' or 'contentment calls', elicited in general in the opposite situations (Collias, 1950; Collias & Joos, 1953). 'Pleasure calls' are undoubtedly heterogeneous and were not studied here; but the 'distress' calls are easily recognizable and could be used readily as a dependent variable.

Material and Methods

Eggs of White Leghorns and Rhode Island Reds were obtained from the Houghton Poultry Research Station, St. Ives, and hatched in an incubator. There were no significant breed differences in the results. Most birds were reared in groups of 12-36 individuals. These were transferred 24 hours after hatching to a large brooding box which was provided with an infra-red lamp for warmth and adequate food and water. The remaining chicks were reared in visual isolation. In these cases the eggs were placed in small cardboard boxes or dacron mesh bags in the incubator. After hatching the chicks were transferred to individual brooding boxes in a soundproof room. They were thus visually but not auditorally isolated from each other; they also heard few noises other than those made by the other chicks, and saw virtually no people.

The birds were tested in a 12-inch square hardboard enclosure, with walls 20 inches high. An infra-red lamp was suspended above the enclosure, and the temperature controlled by varying its height. The temperature was measured on the floor immediately under the lamp; temperature at the edge of the enclosure was about 5° lower.

Experimental Procedures

The experiments were conducted in 5 series:

Series I. Group-reared chicks were tested on days 1 (i.e. 24 ± 2 hours after hatching) to 7 at

temperatures varying from 50° to 110°F. Each chick was removed from the brooding box and placed alone in the pre-heated test apparatus for 10 minutes. The number of distress calls given was counted. The results of this pilot experiment were subsequently analysed in terms of three temperature ranges—below 81°F., 81-100°F., and over 100°F., the number of birds in each group varying from 9 to 20.

Series II a and b. The previous experiment with group-reared chicks was repeated using two standardized temperatures, 60°F. and 110°F. The former can be considered a cold temperature for chicks, the latter near-optimal. In Series IIa each of 12 chicks was tested daily at the lower temperature and 12 others at the higher temperature. In Series IIb each chick was tested once only, 12 naive chicks being tested on each of days 2-7 at the lower temperature, and 12 at the higher.

Series III. Here the chicks used were reared in isolation and tested only once. 12 naive chicks were tested at each of the two temperatures on each of days 1, 3, 6 and 7. This required 96 chicks.

Series IV. In this series, the chicks were reared in groups of 2. In testing, one chick was removed to the test box in the normal way, but observations were made on the bird left behind in the brooder—the only change being the removal of its companion. 12 chicks were tested in this way on days 1 to 7 at 110°F. (the temperature of the brooder).

Series V. Here the chicks were tested in the test box at the higher temperature but a mirror was present, in which the chick could see its image. 12 naive chicks reared in a social group (Series Va) and 12 naive chicks reared in isolation were tested on days 3 and 7 (Series Vb).

Results and Preliminary Discussion

Series I

The results are shown in Fig. 1. Those chicks tested below 80°F. showed a high mean rate of calling throughout, and this did not change significantly with age. Those tested above 100°F. called very little on the first two days, but there was a marked increase on days 3 and 4. The differences between the results for these two temperature ranges were highly significant on every day of testing (t test, $P<0{\cdot}001$). The differences between days 1 and 2 and all subsequent days at the over 100°F. temperature range were also significant ($P<0{\cdot}01$).

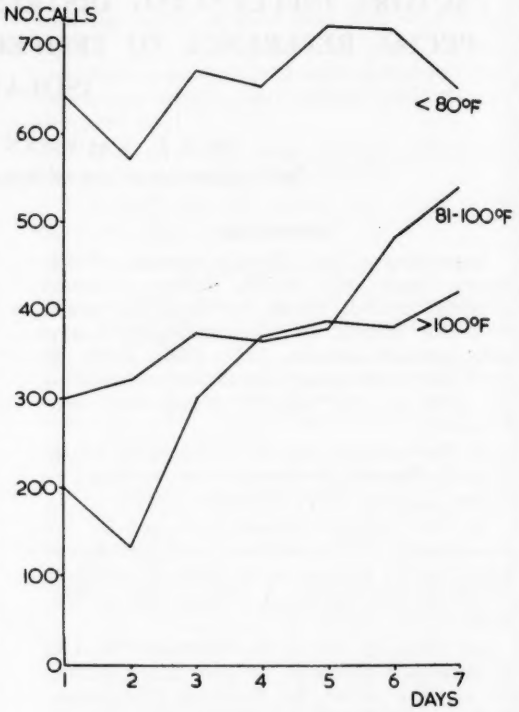


Fig. 1. Series I experiments. Mean number of calls given on successive daily tests at three temperature ranges.

The mean results for the intermediate temperature group were between those of the high and low temperature groups for all days except days 4 and 5, when they approximated to those of the former. The differences between the low and intermediate temperature ranges were significant for every day up to day 6 ($P<0{\cdot}05$) and those between the intermediate and high temperature groups on days 1 and 2 only ($P<0{\cdot}05$). The increase shown by the intermediate temperature groups between days 3, 4 and 5 (taken together) and days 6 and 7 was significant ($P<0{\cdot}01$).

These results indicate that the number of distress calls given increases as the temperature is decreased (within the limits of the experiment). Further, in the high and intermediate temperature groups there is an increase in the number of distress calls given with age—an increase which is absent in the low temperature group, perhaps because they are calling at the maximum rate already.

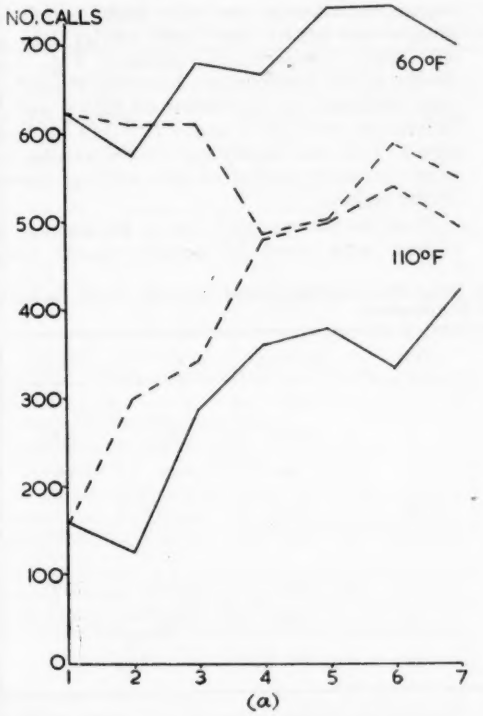


Fig. 2a. Series II experiments. Continuous lines: Mean number of calls given on successive daily tests at 60°F and 110°F. Discontinuous lines: Mean number of calls given by experimentally naive chicks tested once only on one of days 1, 2, 3 . . . . or 7.

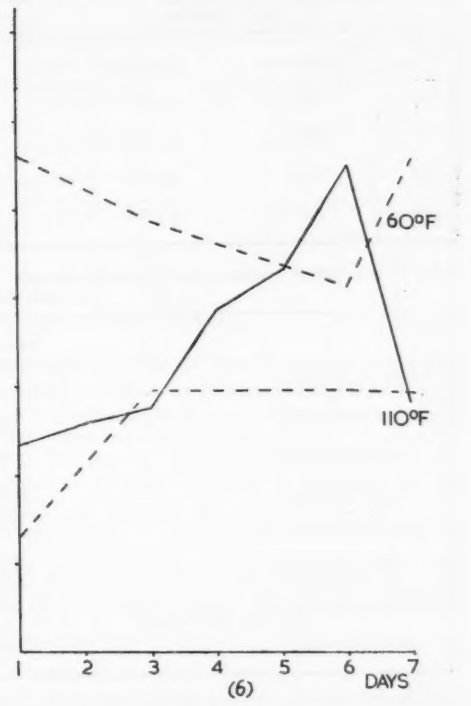


Fig. 2b. Discontinuous lines: Series III experiments. Mean number of calls given by experimentally naive chicks reared in isolation and each tested once only on one of days 1, 3, 6 and 7. Continuous line: Series IV experiments. Chicks reared in groups of 2. Mean number of calls given by chick left in the brooder box when its companion was removed (110°F).

Series II

The results are shown in Fig. 2a. They have been analysed in detail for days 1, 3, 6 and 7.

In the first place, the results obtained in Series I are confirmed. The number of calls given by the birds tested daily (Series IIa) is higher for the low temperature group than for the high temperature group (Difference significant for all of days 1, 3, 6 and 7 at $P<0{\cdot}05$ or better). Further, the number of calls given by the birds tested daily at the lower temperature showed no significant change with age, but the number given by those tested at the higher temperature increased with age (Difference between day 1 and days 6 and 7 significant at $P<0{\cdot}05$ and $0{\cdot}01$ respectively). This causes the two curves to approach each other with age. Similar trends are shown in Series IIb, where naive birds were tested on each day, though the difference between the number of calls given at the two temperatures is even smaller after day 3.

We may now compare the serially tested birds (Series IIa) with the birds tested once only (Series IIb). In general the mean number of calls given by the latter (IIb) was smaller than the number given by the serially tested birds (IIa) at the low temperature, and higher at the high temperature. Representing the effect of age on calling by $x=\alpha+\beta y$, where $y=-3,-1,2$ and 2 on days 1, 3, 6 and 7 respectively, regression lines were calculated (Table I). Partial analysis of variance (Table II) then showed that, at the higher temperature, the difference between IIa and IIb in the rate of increase with age is not

Table I. Relations Between Age and Number of Calls in Test Situation.

Group	Temperature	Regression line
IIa	60°F.	$x=677+22{\cdot}9\,y$
IIa	110°F.	$x=303+41{\cdot}9\,y$
IIb	60°F.	$x=589-8{\cdot}5\,y$
IIb	110°F.	$x=392+71{\cdot}3\,y$

reared in isolation, and the birds reared in groups and tested once only (Series IIb) at the lower temperature (compare Fig. 2a). At the higher temperature, however, the difference, although not significant on days 1 and 3, became so on days 6 and 7 ($P<0{\cdot}01$ in both cases). This was largely due to the smaller increase in mean number of calls with age shown by the isolates.

Thus the increase with age in the number of distress calls given by socially reared birds

Table II. Analysis of Variance for Differences Between Serially Tested Birds and Birds Tested Once only (Series IIa and b) at High and Low Temperatures.

	Sum sq.	D.F.	Mean sq.	F	F0·05
High temperature					
Difference in α	1963	1	1963	3·85	3·95
Differences in β	939	1	939	1·84	3·95
Total residual	46970	92	510·5		
Low temperature					
Differences in α	1838	1	1838	5·27	3·95
Differences in β	1064	1	1064	3·05	3·95
Total residual	32081	92	348·7		

significant, but the higher general mean rate of calling shown by the birds tested once only (IIb) was very nearly significantly different from that of the serially tested chicks (IIa). At the lower temperature the differences are in the opposite direction: the difference between IIa and IIb in rate of increase with age is not quite significant, but the higher general level of the serially tested birds (IIa) is significantly different from that of IIb.

These differences imply that previous experience of the test situation leads to a decrease in response strength if testing is at the higher temperature, and an increase if it is at the lower. In other words, the effect of each experience on the response on a subsequent occasion depends on the extent to which the temperature departed from that preferred. A comparable result has been obtained for the mobbing response of the Chaffinch (*Fringilla coelebs*) (Hinde, 1954, 1961).

Series III

The results are shown in Fig. 2b. There was no significant difference in the number of calls given in the test situation between these birds, tested at the higher temperature is related to their conditions of rearing. In the test situation they are placed alone, and it seems that separation from the social companions becomes an effective causal factor for distress calling after the first three days. This suggests the development of a social bond in the first three days. In the isolates, of course, this factor would not operate. This view was tested further in the subsequent experiments.

Series IV

In this series the chicks were reared in groups of 2: the number of calls given by the bird remaining in the brooder while its companion was removed was recorded. The results are shown in Fig. 2 b. We see that here again the rate of calling increases with age: the increase may be compared with that shown by the group-reared serially tested birds of Series IIa (compare Fig. 2a). Analyses of variance are shown in Table III, and indicate a similar and significant degree of variation between days in both cases ($P<0{\cdot}01$).

To compare the change in number of calls with age between these two groups, linear re-

Table III. Analyses of Variance for the Number of Calls Given by the Group-reared Serially Tested Birds (Series IIa) and the Chicks Reared in Groups of 2 and Tested in the Brooder after Removal of the Companion (Series IV).

Conditions	Factor	Sum sq.	D.F.	Mean sq.	F	F0·05
Group-reared	Chicks	20326	11	1847·8	5·64	1·94
	Days	8389	6	1398·2	4·27	2[24
	Residual	21632	66	327·8		
Group of 2	Chicks	9344	11	849·5	1·41	1·94
	Days	14739	6	2465·5	4·08	2·24
	Residual	39738	66	202·1		

gression lines were fitted $x=\alpha+\beta i$, where $i=-3, -2 \ldots 2, 3$ on days 1, 2, ... 6, 7. The equations obtained were:

Grouped reared $x=300{\cdot}6 + 45{\cdot}2\ i$

Group of 2 $x=355{\cdot}0 + 35{\cdot}5\ i$

A partial analysis of variance (Table IV) indicated no significant difference between the regression coefficients. We can thus conclude

Table IV. Analysis of Variance for Regression Coefficients Relating Number of Calls to Age for Chicks Reared in Large Groups (Series IIa) and in Groups of 2 (Series IV).

Factor	Sum sq.	D.F.	Mean sq.	F
Difference in regression coefficients	158	1	158	0·34
Total residual	61370	132	464·9	

that the increase in number of calls with age shown by the series IV birds is very similar to that shown by the Series IIa ones. The Series IV chicks, however, were tested in their usual environment, were warm, were not handled in any way, and had in fact experienced only one change, the removal of the companion. This confirms the view that separation from the social companion is an effective causal factor for distress calls; the rate of calling in the test situation increases because separation from the social companion becomes an effective causal factor for calling after the first three days.

Series V

Here the chicks were tested in the presence of a mirror. The mean number of calls given for socially reared and isolated birds are shown in Table V, where they are compared with data from Series IIb and III. In neither case is there any significant difference between birds tested with and without a mirror on day 3, but in both cases there were considerable differences on day 7. With the socially reared birds the presence of the mirror was associated with a reduction in the number of distress calls ($P<0{\cdot}001$). Thus the visual stimulus of another chick in the mirror is

Table V. Mean Number of Calls Given in Presence of a Mirror by Socially Reared and Isolated Birds, Compared with Birds Similarly Reared but Tested Without a Mirror (Series IIb and III).

Conditions of rearing	Day	Without mirror	With mirror	Difference $t=$
Social	3	342·2	273·8	0·77
	7	517·2	227·4	5·16
Isolated	3	297·4	298·8	0·02
	7	294·0	461·3	1·82

sufficient to suppress the distress calls. In fact, distress calls seemed to cease as soon as the chick saw its image: these chicks often pecked at the food in the test box and gave pleasure calls, both of which chicks tested without a mirror very rarely did. Thus here again we have confirmation that separation from a social companion is an adequate stimulus for distress calls after the first few days of life (Kaufman, 1960).

The isolates, on the other hand, gave more calls ($0{\cdot}05<P<0{\cdot}01$) in the presence of the mirror than without it. Apparently not only do the isolates not become accustomed to the presence of social companions, but stimuli from a companion actually induce the distress calls in unsocialized chicks.

Conclusions

These experiments confirm that a decrease in environmental temperature and separation from social companions may be important factors in the elicitation of distress calling. The effect of separation from the social companion on the rate of calling was revealed in these experiments by the fourth day after hatching and increased later. With chicks reared socially, visual stimuli from another chick suppressed distress calls after the third day, whereas with chicks reared in isolation, visual stimuli from another chick led not to a decrease in distress calling but to an increase.

We may now consider the relevance of these results to theories about the factors causing the end of the sensitive period.

(*i*) Earlier writers suggested that there was an internally determined waning of the tendency to follow. This view would explain the failure of those older chicks which neither follow nor show fear of the model (Jaynes, 1956) but there is as yet no positive evidence in favour of it.

(ii) The sensitive period is brought to an end because fear responses interfere with following. These fears responses could be evoked by the strange experimental situation, or by the model itself. The present experiments are relevant to this view on the assumption that distress calls come into the category of fear responses. This is so in the sense that they are given in situations from which the chick is trying to escape. In the test situation the chicks frequently tried to leap or fly over the edge of the box. Distress calls are not, of course, the only responses given by chicks in fear-inducing situations—they sometimes give a soft trill, and in seemingly intense fear-provoking situations they freeze.

Our experiments, like those of Hess (1959), indicate that distress calls are given even by one-day-old chicks when moved into a strange pen. Hess found further that the increase in distress calls during the first two days coincided with the end of the sensitive period, and used this as evidence that the development of fear responses was indeed the factor involved. His data are not comparable to ours since he assessed only the presence or absence of distress calls, and not their rate. Guiton (1959), on the other hand, claimed that fear does not develop sufficiently to interfere with following until the chicks are 96 hours old. The discrepancy here may be in part due to the indicator of fear used, and in part to the conditions of testing—Guiton used 30 minutes' training and test sessions, giving time for some birds which showed fear responses initially to switch to following.

It must be emphasized here that the concept of an all-or-none 'critical period', as used by some authors, is misleading. There is rather a gradual change in the probability that imprinting will occur, depending on both the conditions of rearing and the test procedure. For assessing the development of fear responses, Hess used the percentage of chicks giving distress calls in the test situation, and this reached 100 per cent. at 36 hours. In fact, as the present experiments show, this response may increase gradually for several days, though the main causal factors for the calling (change in temperature, absence of the companions, etc.) may not be the same at each age. Our data, which deals with the rate of distress calling per chick, does not indicate an increase between days 1 and 2.

Our results do not bear directly on the relationship between the development of fear responses and the sensitive period, but they do indicate that important factors influencing fear or a similar state are undergoing significant changes during the first few days of life.

(iii) Guiton (1959) found that socialization had an inhibitory effect on the following response. Our data confirm that a strong social bond is formed between chicks, though the lack of significant differences between socially reared birds and isolates before the fourth day might suggest that the bond was formed after 72 hours, the age at which Guiton believed it to influence the following response. Differences in rearing procedure may well account for this, but it would seem important for Guiton's thesis to demonstrate the postulated social bond by an independent means at the relevant age.

Further, our finding that the presence of a mirror in the test pen caused no reduction in distress calls from an isolated chick at 3 days and a (nearly significant) increase at 7 days, seems not to be in harmony with Guiton's view. Guiton found that isolates could still be imprinted at 72 hours, and implies that the tendency to respond to other chicks or to follow is still strong then. Here again, of course, the difference could be due to a difference in the method of testing, and in any case the response of one isolated chick to another at this age involves agonistic patterns as well as social ones.

The inhibitory effect of socialization could operate in a number of ways. For instance, the effect could be a direct one, imprinting on to one object bringing about *per se* a reduction in

responsiveness to others. Alternatively, the reduced following of socially reared birds in imprinting experiments, as compared with isolates, could be due to an interfering appetitive response caused by absence of the social companions, rather than by an increase in the selectivity of the following response itself. In the latter case, Guiton's experimental results would be compatible with the fear hypothesis.

(iii) Moltz (1960) suggests that chicks learn to follow the model because, during the critical period, it becomes associated with a low 'anxiety drive'. This concept is used as an intervening variable for which, it is implied, distress calling may serve as a dependent variable. In support of this view, Moltz & Rosenblum (1958) showed that prior habituation to the test apparatus in the absence of the object to which a strong following response had been attached, produces a decrement in the following response in a later test. The habituation procedure consisted in placing the duckling in the apparatus for an hour before the test. Our experiments suggest that such treatment could lead either to an increase or a decrease in the number of distress calls given, depending in part on the temperature. The temperature in Moltz & Rosenblum's study was not given, and, although they indicate that control subjects were less anxious than the experimentals, no precise details are given.

In summary, some authors suggest that the sensitive period is limited by a reduction in the tendency to follow which is more or less independent of environmental events. This view is difficult to substantiate, and acceptable only faute de mieux. Others emphasize the role of an interfering response—'fear', 'anxiety' or 'distress'—engendered by the test object, the situation, or by separation from companions. It seems likely that different factors may operate in the various species and experimental arrangements which have been used. It is clear, however, that there is an urgent need for an analysis of the various types of 'fear', 'anxiety' and 'distress' responses, and of their interrelation. Our own results suggest the importance of measuring these responses (using the rate of distress calling as well as other criteria) in the same circumstances as those in which the following response is tested, and under a variety of experimental conditions. Only then can their role in determining the duration of the sensitive period be properly tested.

Our results also emphasize the importance of properly controlling temperature, a factor frequently overlooked in imprinting experiments. Indeed, temperature variations might well be used for controlling the level of 'anxiety' in testing both the hypothesis of inhibition by fear responses, and the Moltz hypothesis.

Summary

1. Chicks placed in a strange pen give distress calls at a higher rate if the temperature of the test pen is low than if it is near body temperature.

2. The rate of distress calling of socially reared chicks increases with age at 110°F., significantly so after the third day. At 60°F. there is no such increase, presumably because it is near maximal already.

3. Chicks tested daily at the lower temperature call more than chicks without previous experience of the test situation, but call less (though not significantly so) than naive chicks at the higher temperature.

4. The increase in the rate of calling with age at the higher temperature is not statistically significant in chicks reared in isolation. This suggests that separation from the social companions becomes an important factor in eliciting calling in chicks with social experience. This was confirmed by a number of other experiments.

5. The relevance of these results to various hypotheses about the factors causing the end of the sensitive period for imprinting is considered.

Acknowledgments

Dr. I. C. Kaufman is indebted to the Commonwealth Fund for support during the course of this work. We are also very grateful to Dr. P. Whittle for carrying out the statistical analysis, and to Mr. P. Bateson for his comments on the manuscript.

REFERENCES

Collias, N. E. (1950). The socialization of chicks. *Anat. Rec.* (Suppl.), **108:** Abstract 93.

Collias, N. E. & Joos, M. (1953). The spectographic analysis of sound signals of the domestic fowl. *Behaviour*, **5**, 175-189.

Fabricius, E. (1951). Zur Ethologie junger Anatiden. *Acta. Zool. Fenn.*, **68**, 1-178.

Guiton, P. (1959). Socialization and imprinting in Brown Leghorn chicks. *Anim. Behav.*, **7**, 26-34.

Hess, E. H. (1957). Effects of meprobamate on imprinting in water fowl. *Ann. N.Y. Acad. Sci.*, **67**, 724-732.

Hess, E. H. (1959). Imprinting. *Science*, **130**, 133-141.

Hinde, R. A. (1955). The following response of moorhens and coots. *Brit. J. anim. Behav.*, **3**, 121-2.

Hinde, R. A. (1954, 1961). Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the Chaffinch (*Fringilla coelebs*). I, II and III. *Proc. roy. Soc. B.*, **142**, 306-311, 331-358, and **153**, 398-420.

Hinde, R. A., Thorpe, W. H. & Vince, M. A. (1956.) The following response of young moorhens and coots. *Behaviour*, **9**, 214-242.

Jaynes, J. (1956, 1957). Imprinting: the interaction of learned and innate behaviour. I and II. *J. comp. physiol. Psychol.*, **49**, 201-206, **50**, 6-10.

Kaufman, I. C. (1960). Some ethological studies of social relationships and conflict situations. *J. Amer. psychoanal. Ass.*, **8**, 671-685.

Lorenz, K. (1935). Der Kumpan in der Umwelt des Vogels. *J. Ornithol.*, **83**, 137-213, 289-413.

Moltz, H. (1960). Imprinting: empirical basis and theoretical significance. *Psychol. Bull*, **57**, 291.

Moltz, H. & Rosenblum, L. A. (1958). The relation between drive level and the stability of the following response. *J. comp. physiol. Psychol.*, **51**, 658-661.

Weidmann, U. (1956). Some experiments on the following and flocking reactions of mallard ducklings. *Brit. J. anim. Behav.*, **4**, 78-79.

Accepted for publication 27th February, 1961.

THE STABILITY OF THE DOMESTIC CHICK'S RESPONSE TO VISUAL FLICKER*

BY BARBARA ABERCROMBIE AND H. JAMES
Queen's University, Kingston, Ontario

Previous experiments have shown that if newly hatched chicks are placed in a runway at one end of which a light can be seen to flash on and off, they will rapidly learn to go to that end and stay there. If a stationary object is placed near the flashing light for a number of trials, the chicks will approach and remain near it when it is presented alone without the flashing light (James, 1959). The results of other experiments (James, 1960a and b) suggest that these responses are subject to the same conditions as those which govern conventional imprinting.

The experiments reported in this paper were made in order to find out whether the response to flicker would habituate and whether the approach fixation on the object would extinguish with repeated practice. This question is of interest for the relevance which it may have to two problems: the stability of the following response in conventional imprinting experiments and the resistance of early learning to experimental extinction. Although both of these problems are of some significance in view of the long-term effects which early experience has been shown to exert on the development of adult behaviour, neither of them has received much attention. The only systematic evidence which exists on the stability of the following-response is that of Moltz & Rosenblum (1958). They have shown that, at least for the Peking duck, the effects of imprinting are relatively unstable and, with one test trial a day, begin to disappear within a week after hatching. Fabricius & Boyd (1952) apparently obtained similar results from Mallard ducklings, although they do not give any actual data. Hinde *et al.* (1956), on the other hand, found that coots will continue to follow a moving object upon which they have been imprinted up to about 7 weeks of age, and that moorhens will do so up to about 4 weeks. The authors know of no evidence on habituation in neonatal animals, and very little on the extinction of CR's acquired in infancy. Such evidence as there is, however, suggests that very young animals find it difficult to learn not to respond to a CS which is no longer being reinforced (Panchenkova, 1956; Vince, 1958, 1959, 1960).

*The experiments reported in this paper were made by B.A. in partial fulfilment of the requirement for the M.A. degree at Queen's University. The research was supported by a grant to H.J. from the National Research Council. The second author was responsible for writing the present account of these experiments. We are both grateful to Dr. P. C. Dowdell for his advice on statistics and to Miss Margaret Vince for lending a translation of Panchenkova's (1956) paper.

Experiment I

Method

(1) *Apparatus.* The runway, a 10 ft. long hardboard box (Fig. 1), was essentially similar to that described in the earlier papers. Two timers,

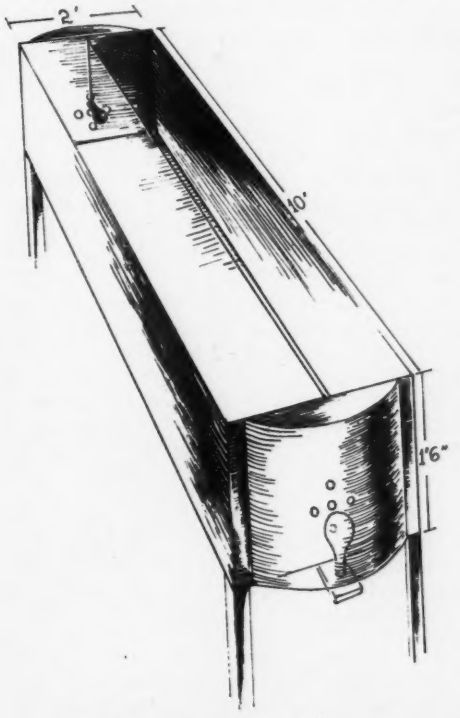


Fig. 1. Schematic drawing of the runway.

placed in another room and inaudible in the experimental room, were used, when appropriate, to make the 100 watt light at one end of the runway or the other (as determined by one of Gellerman's trial orders (Stevens, 1951) flash on and off at the rate of 150 flashes per minute. The "lure", a turquoise polythene ball, was attached to the wall in the middle of the holes through which the flashing light could be seen. The 100 watt light at the opposite end of the runway was lit continuously.

(2) *Subjects.* Sixteen Barred Rock × R.I.R. chicks were obtained from a commercial hatchery. They were isolated from one another immediately on arrival and kept in individual fibreglass mouse cages (Econocages) for the duration of the experiment. Food, water, and light from 4 fluorescent tubes in the ceiling of the room in which they were housed, were continuously available. The chicks were approximately 48 hours old when first introduced into the runway.

(3) *Procedure.* For the first two days of the experiment, all the chicks were given 5 trials a day in the runway, with the light at that end of the runway to which the lure was pinned flashing on and off. They were then divided into 2 matched groups on the basis of their scores during these 10 trials. Group 1 was given 12 further days of training with flicker and stationary lure while Group 2 was given the same number of trials per day (5) with the stationary lure and the lights at *both* ends of the runway lit continuously. Each trial lasted for 5 minutes, and approximately 6 minutes intervened between successive trials.

(4) *Scoring.* At the beginning of each trial, the chick was placed in the middle of the runway and its distance from the lure was then noted every 30 seconds to the nearest 3 inches. Its score for any given trial was taken as the mean of the 10 distances obtained in this way, and could thus vary from 0, indicating the limit of approach, to 10, the limit of avoidance.

Results

The median daily scores for the two groups are given in Fig. 2. It is evident from the upper curve in this figure that, with the measure of performance used in this experiment, no decrement occurs in the approach response when the lure is constantly juxtaposed to a flickering light; the slope of the regression line fitted to the daily mean scores of Group 1 does not differ significantly from zero. The performance of Group 2, which was run under extinction conditions after the first two training days, deteriorated during the second half of the extinction trials. The daily extinction scores of this group correlated significantly with the ordinal number of the extinction day ($r = -0{\cdot}66$; $p = 0{\cdot}01$).

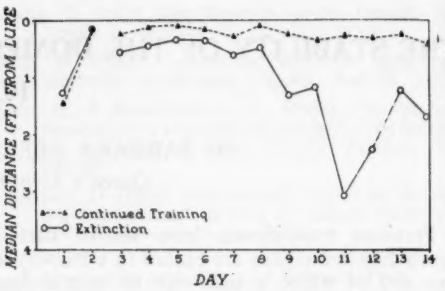


Fig. 2. Median training and extinction scores, Experiment, 1. Both groups were given 5 training trials with flicker and lure on Days 1 and 2. On Days 3-14, one group (solid triangles) continued training with flicker and lure, while the other (open circle) was presented with the lure alone.

Experiment 2

Method

This experiment was essentially an extension of the first one, and provides information about the effects of the number of training trials and of the number of extinction trials, and also about the effects of repeated exposures to a stationary object which is never paired with flicker.

The only difference between this experiment and the previous one was with respect to procedure. Forty-eight chicks were divided at random into eight groups. The treatments given to these groups are listed in Table I, from which it can be seen that there are two major categories of treatment. The experimental groups were given either two (1 a day) or ten (5 a day) training trials, during which they were placed in the runway with the stationary lure and a flickering light at one end and a steady light at the other. The control groups were also given either 2 or 10 trials at the same time, but were exposed only to the stationary lure. For the controls, the lights at *both* ends of the runway were always lit continuously. After two days' training, the extinction procedure was started. For all the chicks the lights at both ends of the runway were lit continuously, and the lure was fixed to one end wall or the other in accordance with a series of

Table I. Treatment during Training and Extinction Phases of Experiment 2.

	Training		Extinction	
Group	No. trials/ day	Condition	No. trials/ day	Condition
IA	1	Stationary lure, next to flicker	1	Stationary lure, no flicker
IB	1	,,	5	,,
IIA	5	,,	1	,,
IIB	5	,,	5	,,
IIIA	1	Stationary lure, no flicker	1	,,
IIIB	1	,,	5	,,
IVA	5	,,	1	,,
IVB	5	,,	5	,,

Gellerman's trial orders. Half the experimental and half the control chicks were given one extinction trial a day; the remainder were given 5 extinction trials a day. Throughout the experiment, where applicable, about 6 minutes intervened between trials. Each trial lasted for 5 minutes.

After 14 days of extinction, all the chicks were assigned to one of 3 main groups.

(*a*) One-third of the chicks (2 from each of Groups IA to IVB) were given four 5-minute trials (2 a day) in which the lure was moved up and down the runway, in a manner similar to that employed in imprinting experiments. (The procedure used in the present experiment was the same as that described previously (James, 1959).)

(*b*) Half of the remaining chicks (2 from each of Groups IA to IVB) were subjected to 10 trials (2 trials a day, 5 minutes for each trial) of 'counter-conditioning', during which the lure was fixed to the end of the runway at which the light was lit continuously, while the light at the opposite end of the runway flashed on and off at the rate of 150 flashes per minute. The remaining 16 chicks were used as controls, and were simply run under the same extinction conditions as had obtained during the preceding 14 days, except that they were given 2 rather than 1 or 5 trials a day. These two groups were then given two test trials, with the stationary lure at one end of the runway and the lights at both ends lit continuously. Another of Gellerman's trial orders was used to determine the end at which the lure should be fixed on any given trial.

Results

(*a*) *Training*. The median scores on the first two days of the experiment, during which the experimental groups were exposed to both lure and flicker and the control groups to the lure alone, are given on the left of Figs. 3 and 4. An analysis of variance of the training scores confirms what will be obvious from an inspection of these two figures. The only treatment providing a significant source of variation was that of flicker vs. no flicker ($F=95{\cdot}06$, 1 and 44 df., $p<0{\cdot}01$).

(*b*) *Extinction*. The median scores of the various groups during the extinction part of the experiment, when the lure was stationary and the lights at both ends of the runway were lit contiouously, are given in the main portion of Figs. 3 and 4. The results of an analysis of variance performed on the extinction scores are given in Table II. From this it will be seen that the differences in treatments during training gave rise to

Table II. Summary of Analysis of Extinction Scores, Experiment 2.

Source	df.	MS	F
Extinction procedure (E)	1	120,626	2·56
Training procedure (T)	3	429,499	9·13*
E x T	3	84,384	1·79
Between groups	7	237,468	
Within groups	40	47,000	

*$p<{\cdot}01$

significant differences between the groups during extinction, while the number of extinction trials given per day did not. T-tests were made of the differences between the means of the various groups, with the results shown in Table III. From this table it will be seen that while exposure to flicker during the two training days produced a higher level of performance during the extinction trials, the number of training trials (within the limits tested) was of no consequence.

Inspection of the individual data suggested that systematic changes in performance were

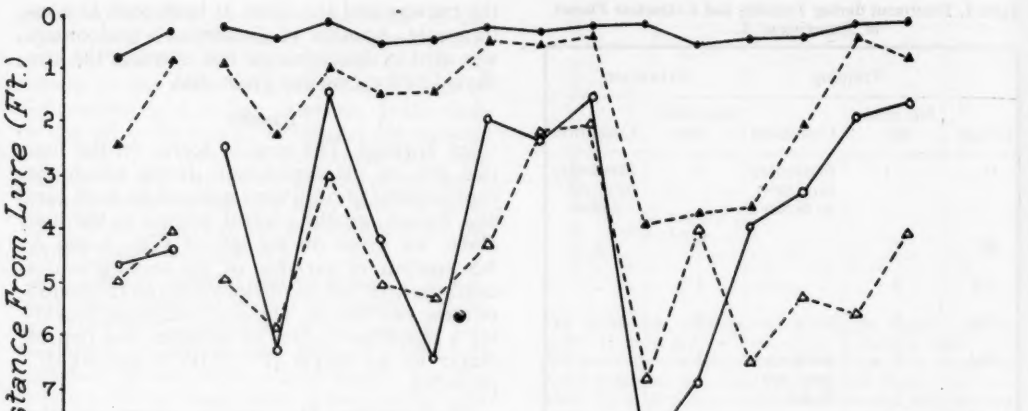


Fig. 3. Median training (Days 1 and 2) and extinction (Days 3-16) scores, Experiment 2. The experimental groups were exposed to both flicker and lure during training, the controls to the lure alone. During extinction all chicks were exposed to the lure alone for one trial a day.

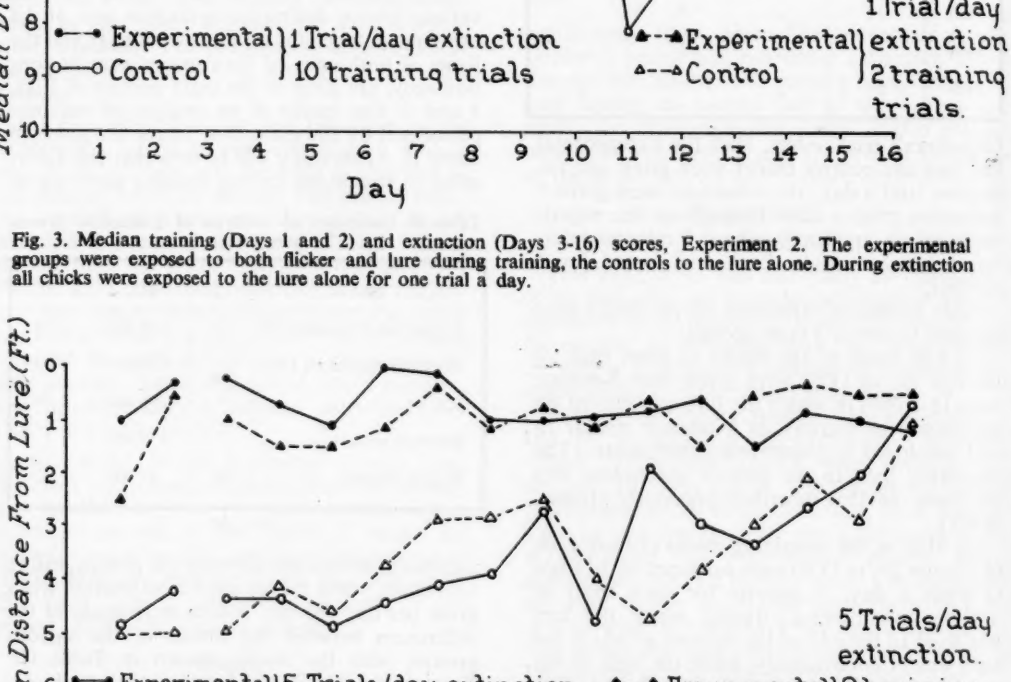


Fig. 4. Median training (Days 1 and 2) and extinction (Days 3-16) scores, Experiment 2. The experimental group were exposed to both flicker and lure during training, the controls to the lure alone. During extinction, all chicks were exposed to the lure alone for five trials a day.

Table III. Significance of Differences Between Mean Extinction Scores, Experiment 2.

Groups	t	p
Group I vs. Group II	1·16	n.s.
Group I vs. Group III	3·16	$<$·01
Group II vs. Group IV	4·21	$<$·01
Group III vs. Group IV	$<$1·0	n.s.

occurring in the performance of certain groups during the extinction trials. Accordingly, correlations were computed between the daily extinction scores of each of the groups and the ordinal number of the extinction day. There was a significant ($p<·01$) *improvement* in the performance of those control groups (IIIB and IVB) which were given 5 trials a day during the extinction period ($r=0·72$ and 0·81 respectively), and a similar improvement in one of the experimental groups (IB) which was given one trial a day during training and 5 trials a day during extinction ($r=0·75$). There is also a suggestion in the statistical analysis that the performance of Group IIB, which was given the same treatment as Group 2 in Experiment 1 (5 trials a day both during training with flicker and during extinction) *deteriorated* during extinction ($r=-0·55$; $p=0·05$). None of the correlations approached significance in the case of any of the remaining groups, all of which, it will be noted, were given one trial a day during the extinction period.

(*c*) *Test with Moving Lure.* Eight of the chicks (half of them from the original control groups) used in this test were still approaching the stationary lure consistently at the end of the 14 days of extinction. While none of these chicks followed the moving lure the first time it was presented to them on the 17th day of the experiment, all of them were doing so by the end of the 18th day (4th test trial). The remaining 8 chicks had either lost their preference for the end of the runway marked by the stationary lure by the 16th day of the experiment, or had never acquired one. Of these chicks, only one (on the last test trial with the moving lure) followed the lure with any consistency. The others either persisted in the position habit which they had adopted during extinction, or actively avoided the lure when it moved.

(*d*) *Effects of* '*Counter-conditioning*'. It will be recalled that two chicks from each of the groups listed in Table I were subjected to 10 trials in which the lure and the flickering light were placed at opposite ends of the runway ('counter-conditioning'), while two further chicks from each of these groups were used as controls (lure, but no flicker). All these chicks were then given two test trials in which the stationary lure was presented alone at one end of the runway or the other. The approach fixation was as strong after the counter-conditioning trials as before, even though there was some disturbance, *during* the counter-conditioning trials, in the performance of the chicks which had acquired and maintained an approach fixation during the preceding 16 days.

Discussion

There are three main sources from which hypotheses concerning the nature of the chick's response to visual flicker may be derived. Firstly, this response may be elicited by the same proximal stimulus as the following-response in conventional imprinting experiments, and thus may depend upon essentially the same mechanisms. While it was suggested in a previous paper (James, 1959) that the structure of the chick's retina is such that the image of a moving object would give rise to the same kind of on/off effect as would a flickering light (cf. Pumphrey, 1948; Schneirla, 1959, p. 15), this hypothesis has yet to be tested, and should, therefore, be treated with some reserve. As has already been mentioned, however, the flicker response does seem to be subject to the same conditions as the following-response. In particular, the ease with which it can be acquired appears to diminish with age at first exposure to flicker (James, 1960a), its acquisition is prevented if chicks are reared together rather than in isolation (James, 1960b), and it is 'forgotten' if daily practice trials are not given (James, in preparation).

Secondly, the response to flicker may be related to other photoperiodic responses which have been studied extensively in birds (for reviews of the subject see Withrow, 1959). One or two of these studies (cf. Burger, Bissonnette & Doolittle, 1942) have used flicker rates comparable with our own to induce the physiological changes which accompany the increase in premigratory nocturnal activity characteristic of certain birds, (and which can also be produced in domestic hens and ducks). Little evidence is available concerning the exact relation between these physiological effects and level of behavioural activity, but it seems likely that both are under the control of the hypothalamus (Benoit, 1956;

Nalbandov & Card, 1943), which is, in turn, directly influenced by photoperiodic changes (Benoit, 1956). It may, therefore, be tentatively suggested that intermittent light serves the same function in avian behaviour as, for instance, the hunger drive in mammals; that is it lowers the threshold of responsiveness to environmental change (Campbell & Sheffield, 1953).

Thirdly, the response to flicker may be regarded as a form of early learning. The idea that imprinting and learning may be related has been received with some disfavour in recent reviews of the subject (Hess, 1959). It seems that this has largely been due to an over-readiness to assume that early learning in chicks can be directly compared with adult learning in rats, and that learning in general can adequately be accounted for in terms of the principles of either classical or instrumental conditioning. Even the studies of sensory deprivation in infancy, which form the bulk of our knowledge of early learning, indicate that the problem is more complex than this, and it would seem that fruitful ideas for the analysis of early learning and imprinting are more likely to come from a close study of recent work on sensory preconditioning, sensory change as a reinforcer, etc., than from a doctrinaire belief in the unity (or disunity) of the learning process.

The three approaches which are outlined above are clearly not mutually incompatible, and by making some further assumptions concerning the relation between imprinting and early learning, and the nature of the motivating conditions for these processes, it would be possible to fit them together into a single 'theory'. The number of assumptions, however, is rapidly approaching the number of facts which exist to be explained, and the present discussion will therefore be limited to pointing out some of the implications of the experimental results for these various points of view.

(i) The Development of an Approach Fixation in the Absence of Flicker.

The results from the control groups (Fig. 4) which were given 5 trials a day during the extinction part of Experiment 2 indicate that neither movement nor flicker are necessary for the establishment of an approach fixation. Although they had never been exposed to flicker and had never seen the lure move, two thirds of the chicks in each of these 2 groups gradually learned to approach and stay near the lure; and when the lure was moved for the first time on the 17th day of the experiment, they learned to follow it as closely as did the chicks from the experimental groups.

Apart from a similar observation which was reported incidentally in a previous paper (James, 1959), and an experiment by Hess (1959, pp. 44 and 49) in which 3-day-old chicks were shown to prefer a stationary stimulus to which they had been exposed continuously on the previous day, there is no other evidence available on this effect. Superficially, it resembles one which Gibson and her colleagues have described in a number of recent papers (Gibson & Walk, 1956; Gibson *et al.*, 1958; Walk *et al.*, 1959). They have shown that rats, reared in cages to the walls of which cutout patterns were attached, later discriminated these patterns more readily than rats reared under control conditions. When the figures were painted on a flat background, instead of being cut out of sheet metal, no facilitation was observed (Walk *et al.*, 1959). Walk explains this difference in terms of the greater 'attention-getting value' of the cutouts. This concept of 'attention-getting' cannot, however, be used without further elaboration, to explain either the Gibson facilitation effects in rats or the approach fixation which established itself in the 5 trial-a-day control chicks. As Arnoult (1957) points out in connection with a closely related problem, 'the usefulness of an explanation based upon *attention* to cues will be slight until it is possible to specify more adequately what attention is and to make some guesses about how it operates to facilitate recognition or memory' (p. 347). Whether or not the Gibson effect and the approach fixation are allied phenomena, the experimental problem is the same in each case, and the first step in its analysis is to relate 'the discriminable attributes of the stimulus both to its physical structure and to various experiential factors' (Arnoult, *ibid.*, p. 349).

(ii) The Role of Visual Flicker in the Development and Maintenance of the Approach Fixation

Although the approach fixation can be established without pairing the lure with flicker, it is abundantly clear that it is learned much more quickly if the lure is placed near an intermittent light source during the early trials (Figs. 3 and 4), and that the response is more stable if the flicker is present on *all* the trials (Fig. 2).

There are at least three directions in which an explanation for these effects may be sought. First, it may be that flicker adds to the 'attention-

getting' value of the lure. Second, flicker may serve as a non-specific arousal stimulus, with an energizing rather than a directive function. While there are one or two experiments whose results are consistent with the view that level of arousal is an important determinant of the strength of conventional imprinting (Moltz *et al.*, 1959; cf. also Hess' (1959) 'Law of Effort'), the grounds for relating flicker to activity level are, as was noted above, somewhat tenuous. The problem, however, is one which is amenable to experiment, and we are at present trying to gather some evidence on it. Third, it is possible that intermittent light acts as a reinforcer, in the same way as the onset of illumination is known to do in operant conditioning and other forms of learning in rats (cf. Hurwitz, 1956; Levin & Forgays, 1960). The atypical temporal relation between the CS (lure) and UCS (flicker) gives rise to some rather obvious conceptual difficulties in connection with this particular analogy.

(iii) Resistance of the Approach Fixation to Extinction

As was remarked in the introduction, there are some discrepancies in the literature concerning the stability of conventional imprinting. Since these are possibly due, in part at least, to species differences (Moltz & Rosenblum, 1958; Klopfer, 1956), and since no data appear to be available on the stability of the following response in the domestic chick, direct comparison with the present results is not possible.

The simplest explanation which is at present available for the persistence of the approach fixation with daily practice is one based on a competition of response theory of extinction. While the evidence is not entirely consistent (Haggard, 1959), some support can be found for the view that learning in adult mammals is particularly resistant to extinction if competing responses are not available during the extinction trials (Maatsch, 1959). The chicks used in our experiments have a relatively limited opportunity to acquire responses which could interfere with approach to lure. Generally speaking, they respond positively to the intermittent light on the first trial on which they are exposed to it, and it is rare to see a chick engage in any kind of behaviour which could be described as trial and error before it approaches the flicker end of the runway. On these grounds, therefore, one might expect the approach response to the lure to be fairly persistent. The same explanation would also apply to the finding (Abercrombie & James, in preparation) that an approach response based upon hunger motivaton is as resistant to extinction as one which is based upon flicker.

Summary

Two experiments with Barred Rock × R.I.R. chicks were described on the effect of repeatedly eliciting the approach response to (*a*) an intermittent light source and (*b*) a stimulus which had previously been paired with an intermittent light. The main results were as follows:

1. The chicks rapidly learned to approach and stay near that end of the runway at which an intermittent light could be seen. Once this response had been acquired, it could be elicited repeatedly (5 five-minute trials a day for at least 12 days) without any sign of decrement.

2. A stationary object was placed at the same end of the runway as the intermittent light for the first 2 days (training). The object was then presented alone in the runway on days 3-16, without the intermittent light (extinction), with the following results:

(*a*) With 5 training trials a day on the first 2 days, and 5 extinction trials a day on the 3rd and subsequent days, some evidence was obtained, in both experiments, of a gradual decline in responsiveness to the stationary object.

(*b*) When only 2 training trials (1 a day) were given, followed by 5 extinction trials a day, the chicks appeared to become more responsive to the stationary object as the number of extinction trials increased.

(*c*) When only 1 extinction trial a day was given, the level of performance reached during training was maintained without significant change during extinction.

3. Chicks which had been given a sufficient number of trials per day (5) slowly learned to approach that end of the runway at which the stationary object could be seen, even though it was never paired with an intermittent light.

4. Chicks which had acquired and maintained an approach response to the object when it was stationary rapidly learned to follow it up and down the runway on the 17th and 18th days of the experiment. With one exception, chicks which had not acquired the response to the stationary object, or had lost it during the extinction trials, failed to follow the object when it was moved up and down the runway.

It is pointed out that there are at least 3 fields of enquiry which may be relevant to an understanding of the chick's response to visual flicker:

imprinting, photoperiodism and early learning. Some of the implications of existing knowledge in these fields for the results of the present experiments are briefly discussed.

REFERENCES

Arnoult, M. D. (1957). Stimulus predifferentiation: Some generalizations and hypotheses. *Psychol. Bull.*, **54,** 339-350.

Benoit, J. (1956). Etats physiologiques et instinct de reproduction chez les oiseaux. In: *L'Instinct dans le Comportement des Animaux et de l'Homme.* Paris: Masson.

Burger, J. W., Bissonnette, T. H. & Doolittle, H. D. (1942). Some effects of flashing light on testicular activation in the male Starling (*Sturnus vulgaris*). *J. exp. Zool.*, **90,** 73-82.

Campbell, B. A. & Sheffield, F. D. (1953). Relation of random activity to food deprivation. *J. comp. physiol. Psychol.*, **46,** 320-322.

Fabricius, E. & Boyd, H. (1952-3). Experiments on the following-reaction of ducklings. *Wildfowl Trust Ann. Rept.*

Gibson, Eleanor J. & Walk, R. D. (1956). The effect of prolonged exposure to visually presented patterns on learning to discriminate them. *J. comp. physiol. Psychol.*, **49,** 239-242.

Gibson, Eleanor J., Walk, R. D., Pick, H. L. Jr. & Tighe, T. J. (1958). The effect of prolonged exposure to visual patterns on learning to discriminate similar and different patterns. *J. comp. physiol. Psychol.*, **51,** 584-587.

Haggard, D. F. (1959). Experimental extinction as a function of the type of response elicited in the goal box. *Psychol. Rec.*, **9,** 93-98.

Hess, E. H. (1959a). Imprinting. *Science*, **130,** 133-141.

Hess, E. H. (1959b). The relationship between imprinting and motivation. In: Jones, M. R. (Ed.), *Nebraska Symposium on Motivation.* Lincoln: Univ. Nebraska Press.

Hinde, R. A., Thorpe, W. H. & Vince, M. A. (1956). The following response of young coots and moorhens. *Behaviour*, **9,** 214-242.

Hurwitz, H. M. B. (1956). Conditioned responses in rats reinforced by light, *Brit. J. anim. Behav.*, **4,** 31-33.

James, H. (1959). Flicker: an unconditioned stimulus for imprinting. *Canad. J. Psychol.*, **13,** 59-67.

James, H. (1960a). Imprinting with visual flicker: evidence for a critical period. *Canad. J. Psychol.*, **14,** 13-20.

James, H. (1960b). Social inhibition of the domestic chick's response to visual flicker. *Anim. Behav.*, **8,** 223-224.

Klopfer, P. H. (1956). Comments concerning the age at which imprinting occurs. *Wilson Bull.*, **68,** 320-321.

Levin, H. & Forgays, D. G. (1960). Sensory change as immediate and delayed reinforcement for maze learning. *J. comp. physiol. Psychol.*, **53,** 194-196.

Maatsch, J. L. (1959). Learning and fixation after a single shock trial. *J. comp. physiol. Psychol.*, **52,** 408-410.

Moltz, H. & Rosenblum, L. A. (1958). Imprinting and associative learning: the stability of the following response in Peking ducks. *J. comp. physiol. Psychol.*, **51,** 580-583.

Moltz, H., Rosenblum, L. & Halikas, Nina (1959). Imprinting and level of anxiety. *J. comp. physiol. Psychol.*, **52,** 240-244.

Nalbandov, A. V. & Card, L. E. (1943). Effect of hypophysectomy on growing chicks. *J. exp. Zool.*, **94,** 387-414.

Panchenkova, E. F. (1956). The ontogenetic development of conditioned reflexes in the white rat. *Zhurnal Visshei Nerv'noi Deyatelnosti*, **6,** 312-318.

Pumphrey, R. J. (1948). The sense organs of birds. *Ibis*, **90,** 171-199.

Schneirla, T. C. (1959). An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In Jones, M. R. (Ed.), *Nebraska Symposium on Motivation.* Lincoln: Univ. Nebraska Press.

Stevens, S. S. (Ed.) (1951). *Handbook of Experimental Psychology.* New York: Wiley.

Vince, M. A. (1960). Developmental changes in responsiveness in the Great Tit (*Parus major*). *Behaviour*, **15,** 219-243.

Vince, M. A. (1958). String-pulling in birds. 2. Differences related to age in greenfinches, chaffinches and canaries. *Anim. Behav.*, **6,** 53-59.

Vince, M. A. (1959). Effects of age and experience on the establishment of internal inhibition in finches. *Brit. J. Psychol.*, **50,** 136-144.

Vince, M. A. (1960). Developmental changes in responsiveness in the Great Tit (*Parus major*). *Behaviour*, **15,** 219-243.

Vince, M. A. (1961). Developmental changes in learning capacity. Ch. IX in Thorpe, W. H. & Zangwill, O. L. (Eds.): *Current Problems in Animal Behaviour.* Cambridge.

Walk, R. D., Gibson, Eleanor J., Pick, H. L. Jr. & Tighe, T. J. (1959). The effectiveness of prolonged exposure to cutouts vs. painted patterns for facilitation of discrimination. *J. Comp. physiol. Psychol.*, **52,** 519-521.

Withrow, R. B. (Ed.) (1959). Photoperiodism and related phenomena in plants and animals. *Amer. Ass. Adv. Sci. Public.*, No. 55.

Accepted for publication 5th October, 1960.

ECOLOGY OF INSECT SWARMS. I. EXPERIMENTAL STUDIES OF THE BEHAVIOUR OF *Anarete near felti* Pritchard IN ARTIFICIALLY INDUCED SWARMS (Cecidomyiidae, Diptera)*‡

By H. C. CHIANG†

Department of Biology, University of Minnesota, Duluth, Minnesota

Abstract

The relations between some characteristics of the source of attraction and the swarming of the midge, *Anarete near felti* Pritchard were described. White Bristol boards against a dark background were used as the source of attraction. It was found that the degree of attraction varied with the size and the position of the boards, the general lighting, and the proximity, intensity and position of other sources of attraction. An association between swarming and mating was suggested.

Introduction

Swarming of insects is a familiar sight in the field and around the homes. Midges being attracted to bright surfaces, including persons with light-coloured hats or shirts, is also a common experience for many who spend time outdoors. Aspects of swarming of various insects, including bees, ants, gnats and mosquitoes, have been studied rather intensively. Very little, however, has been reported on the relation between the characteristics of the source of attraction and the swarming behaviour of midges.

It was noted in the summer of 1958 that the midge, *Anarete near felti* Pritchard was attracted to reflective surfaces such as a piece of white paper, and that it showed a peculiar orientation to the source of attraction. When the midges appeared again in the summer of 1959, more systematic observations were made in order to contribute to our knowledge of the general problem of swarming among the insects.

Methods

The observations were made during the late summer in 1959 in Waseca, Minnesota (latitude 44°05′ N; longitude, 93°30′ E.). The locale was along the alleyways and other clearings in the experimental plots of field corn, *Zea mays* L. Most records were secured between 1000 and 1400 hours (Central Standard time, U.S.A.) on sunny days. The midges were most active during this period which was the warmest and brightest. Such periods are preferred also by the valley black gnat for swarming (Fontaine *et al.*, 1957).

The insect was found to be attracted to bright surfaces. In this study, white Bristol boards of five different sizes (2 × 3 in. to 8 × 12 in.) against a large black Bristol board (22 × 28 in.) were used as the source of attraction. The boards were placed at the ground level. Caution was taken to avoid any shadow of corn plants or weeds. The temperature was recorded for most of the observations, but no attempt was made in this paper to analyze the effect of temperature on swarming.

Orientation of the Swarms

Study No. 1. When a piece of white board of an adequate size was placed on a black background, it was noted that the swarm was formed on the east edge during the morning and on the west edge during the afternoon. In other words, the swarm was formed always along the edge of the white board nearest to the sun (Fig. 1). When the sun was at or near the zenith, however, the midges swarmed over the entire area of the board. It was further noted that when the board was oriented so that one corner was nearest to the sun, the swarm was then formed at that corner and at a greater density.

Study No. 2. In order to determine whether the particular orientation was due to a daily rhythm on the part of the insect, or was a response to the reflection (and/or diffusion) of sunlight, the white board was tilted to different angles in relation to the sun. During either the morning or the afternoon, if the board was tilted to receive the sun's rays from a perpendicular direction, the midges reacted as though it was noon, namely, swarmed over the entire surface of the board. Upon further tilting, the swarm moved to the top edge which was nearest to the sun.

*This study is partially supported by a research grant (B-5154) from the U.S. National Science Foundation to the University of Minnesota.

‡Paper No. 4312, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul, 1, Minnesota.

†Department of Entomology and Economic Zoology, University of Minnesota, St. Paul, Minnesota.

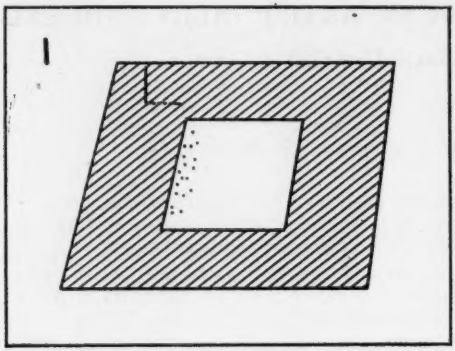


Fig. 1. The distribution of midges over a white Bristol board with a black background. White areas, white board; hatched areas, black background; dots, midges. Short vertical line at the upper left represents an upright stick. The direction of the shadow of the stick indicates the position of the sun. Left side of the graph represents the east, right side, west.

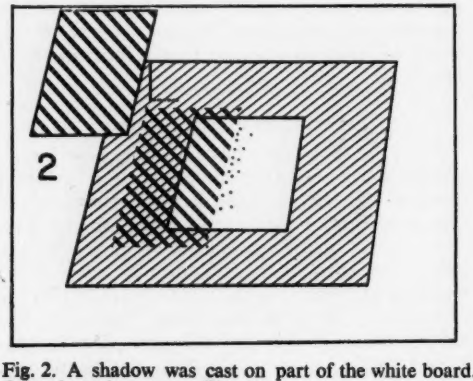


Fig. 2. A shadow was cast on part of the white board. Other legends same as Fig. 1.

The results of the above two studies suggest that the orientation of the swarm was affected by the position of the board in relation to that of the sun, and that the actual hour of the day or the actual position of the sun was not significant.

Study No. 3. An additional observation was made by casting a shadow on the swarm. It was noted that the midges moved out of the shadowed area and swarmed just beyond it (Fig. 2). This phenomenon was of particular interest when we consider the fact that during periods when both the board and the background were shadowed by thin clouds, the midges could still distinguish, and preferred, the edge of the white board nearest to the sun. These facts suggested that the midges preferred the line of demarcation, or the strongest contrast in light intensity possible. But why they preferred the edge nearest to the sun was not understood. The analysis of the physical and physiological bases of these phenomena presents a challenge.

The source of attraction for insects to form a swarm has been termed "swarm markers." Two types of swarm markers have been observed in different insects. The first type involves patterns of lighting on a horizontal level, e.g. on the ground surface. The marker consists of a contrast in lighting: a dark area on a light background or a light area on a dark background. In observing the mosquito, *Aedes punctor*, which formed swarms several feet above the grass tops, Frohne (1953) reported that tramping down the grass under a swarm making a dark "hole" regularly resulted in a shift of the swarm, and that slipping a white sheet under a swarm broke it up at once. The same author also observed the light reaction of the midge *Anatyolynia algena* (Coq.), and reported, however, that a white sheet on the ground initiated swarms of this insect. Different reactions have been found also in closely related species. Downes (1955) reported that *Culicoides nubeculosus* (Meigen) was attracted to dark areas whereas *C. riethi* Kieffer was attracted to white areas. The difference in light reaction might be related to the normal daily rhythm of warming activities of the insects. Both the mosquito *A. punctor* and the midge *C. nubeculosus* were active at dusk, whereas the midge *C. reithi* (in Downes study) and *A. near felti* Pritchard were active during bright day light. (No information was available regarding the rhythm of the midge *A. algena*). The possible importance of intrinsic factors within a species, however, is not to be ruled out. Cambournac & Hill (1940) reported that swarms of *Anopheles maculipennis* showed a preference for different light intensities. They observed a swarm near the window of a stable and one in a dark region in the centre of a barn at the same time.

The second type of swarm marker involves a protruding upright object. Ants (Chapman, 1957), flies (Dodge & Seago, 1954), may beetles (Schneider, 1952), and Papilio butterflies (Merritt, 1952) have been observed to swarm at mountain summits. Midges *Serromyia femorata* and *Forcipomyia cilipes* (Downes, 1955) were reported to swarm about trees. Such insects are considered to show a positive "hypsotaxis", or an attraction toward the most prominent sil-

houette on the horizon. It seems to the present author that "hypsotaxis" might merely be another manifestation of the preference of a demarcation of contrasting light intensities as shown by the midges in the present study. Thus, Downes suggested that the difference between insects using horizontal swarm markers and those using vertical markers is that the former use the ventrally directed ommatidia of their compound eyes whereas the latter use the lateral elements.

Another aspect of the swarming behaviour is in regard to the position of the swarm in relation to the positions of the light source and the swarm marker. In the present study, the midge swarmed nearest to the source of light. In the mosquito, *Mansonia perturbans*, however, Snow & Pickard (1959) observed that at dusk the mosquitoes swarmed between the collector's head and an overhead canopy, but mainly away from the western sky where scanty light still prevailed. The above difference could be the result of the difference in the normal behaviour pattern of the insects involved; the midge is diurnal while the mosquito is crepuscular. More studies, comparative as well as experimental, are needed to adequately explain these phenomena.

Pattern of Flight and Alighting

Study No. 4. The individual midges within a swarm flew in a zigzag manner, both vertically and horizontally. The distance of the path in any one direction was usually within one inch. They swarmed only 2-3 inches above the board.

When the air was very still, the swarm as a whole moved only a little in relation to the edge of the board. When only one midge was flying, such as in the case of over a very small board, under a weak lighting, or before others appeared on the scene, it usually scanned the entire edge of the board. When the swarm increased in size, it became more and more compact and stationary. As mentioned earlier, the midges also scanned over the entire area of the board when the sun is at the zenith. In such case, the swarm was usually rather loose and fluid.

The midges alighted under the influence of even a very slight breeze. They usually alighted on the white board. If the breeze were stronger, they would alight on the black background board 1-3 inches away from the white board. It was observed that when the midges alighted on the white board most of them faced the direction of the sun. When they alighted away from the white board, however, most of them faced the direction of the wind. These facts suggest (1) that the midges faced the sun during flight, and (2) that when the wind was strong enough to carry the midges off their swarming location, they turned into the wind and actively alighted facing the wind. Downes, however, reported that the midges of Culicoides in swarm always headed upwind. It is true that most of the species he observed were active at dusk. This might suggest that the midges always orient toward wind under diffused lighting. Yet, a few of his observations were made during daylight hours. No adequate explanation could be offered for the discrepancy existing between the conclusions of Downes and the present study.

Degree of Attraction of White Boards

While there is an extensive literature on the orientation of insect swarms, little has been reported regarding the size of swarms. The only record on the relation between the size of the swarm and the size of the swarm marker expressed in quantitative terms, is by Downes (1955) who stated, "Those (swarms) over pads of cowdung were little more than 1 ft. above the surface and consisted of a dozen or so individuals, whereas those over patches of dark mud several square feet in area averaged 30 to 50 insects, and the base of the swarm was at a height of 2 ft. to 4 ft. and the column extended upward to about 8 ft." Although some of the species under his observation could be induced to swarm with artificial arrangements, Downes did not pursue this aspect.

The species dealt with in the present study showed three characteristics: (1) the swarms were small, (2) they were formed near the ground surface, and (3) they could be induced artificially. This combination offered a unique opportunity for a detailed study of the size relation. Three observations were made in this respect. The size of the swarm-marker was varied simply by using white boards of different sizes: 2×3, 3×4, 4×6, 6×8 ,8×12 inches, or 6, 12, 24, 48, 96 square inches.

Study No. 5. Speed of response of midges in relation to board size was studied by placing a board of a given size, and recording the time before the first midge appeared. Boards of 5 different sizes were placed one at a time in a random sequence. An interval of at least 2 minutes was maintained between two observations. The observations were repeated 5 times, so 5 readings were obtained for each board size.

Table I. Speed of Response in Relation to Board Size.

Board size	Time (number of seconds) between the placing of the board and the appearance of the first midge.					
	Five readings					Average
2 × 3 in.*	—	—	—	—	—	no midge appeared
3 × 4 in.	33	62	87	30	40	50·4
4 × 6 in.	8	4	5	7	4	5·6
6 × 8 in.	7	2	5	3	2	4·2
8 × 12 in.	1	3	2	1	2	1·8

*Observations were continued for 2 minutes.

This set of observations was carried on during the noon hours of the same day, August 19th, 1959. The results are presented in Table I. The sun during that period was bright and an average light intensity of 500 ft.-c. was recorded.*

These data show the following points: (1) With the largest board used, the response of the midges was almost instantaneous. This fact suggested that the midges must have been in the vicinity during the time of study. (2) The speed of response was directly related to the size of the board. (3) There was a minimum size of the board which was attractive to midges. Under the given conditions, the minimum size seemed to be 3×4 inches.

Study No. 6. A series of observations was made to determine the relation between the size of the board and the number of midges attracted. This was done by estimating the number of midges swarming above a board of a given size, from time to time for 5 minutes. In most cases, the maximum number was reached within 5 minutes. An attempt to improve the estimates has been made by placing a hood (consisted of a wooden frame and "Saran Wrap" covering, and of the size of the background board and 1 foot high) over the swarm after the maximum size had been reached, and counting the number of midges within the hood. It was found, however, that some midges always escaped before the hood could be placed. Thus this practice was discontinued in favour of visual estimation. It was felt that by limiting the observations to swarms of 20 or fewer midges, the estimates were fairly accurate. Furthermore, it was noted that the midges settled down on the board at even a slight and momentary breeze. Accurate counts were possible during such moments. The estimates checked very well (± 1) with the actual counts when such counts were available.

The results of four replicates obtained during the noon hours on two different days are shown in Table II.

Table II. Relation Between the Number of Midges in the Swarm and the Size of the Board.

Board size	Number of midges in the swarm				
	Four readings				Average
2 × 3 in.	0	0	2	0	0·7
3 × 4 in.	1	4	5	1	3·3
4 × 6 in.	8	8	10	8	8·7
6 × 8 in.	12	14	15	12	13·7
8 × 12 in.	14	19	20	15	17·7

These data show the following points: (1) The number of midges attracted to a board of a certain size varied appreciably on different days. This might have been due to the varying degrees of general abundance and activity during different days. (2) In spite of the variation, there was a direct relationship between the size of the swarm and the size of the board. It is not impossible that the presence of midges might have attracted more midges, as suggested by Downes (1955) in the case of *Culicoides*. But even if this had been the case, the size of the board was still critical in setting the maximum size of the swarm. (3) In three out of the four trials, the 2×3-inch board attracted no midges during a period of 5 minutes.

*A General Electric exposure meter (type DW-68) was used. The measurements were made by holding the instrument in a vertical position, with the cover closed, and about one foot above the centre of the white board.

Study No. 7. In order to check whether the minimum attractive size may vary under different degrees of lighting, some additional observations were made whenever the occasions arose. At 1350 hour on September 1st, 1959, it was cloudy (light 220 ft-c.; temperature, 80°F.), and for 12 minutes no midge appeared on the 8×12-inch board. At 1402 hour, the sun broke out, and almost instantly 2 midges appeared. This fact suggested that a board of a given size may be either above or below the minimum attractive size, depending upon the light intensity.

In another instance, the 8×12-inch board attracted 15 midges under a bright sun on one day, but only 6 under a hazy sun the following day. On this second day, a board 23×28 inches in size was necessary to attract 15 midges. This fact again suggested the same relationship. Thus it was clear that the attraction of a surface depended on both the size of the surface and the general lighting conditions. More work is needed to establish this relationship on a mathematical basis.

Mating During Swarming

Study No. 8. It has been observed in mosquitoes (Roth, 1948) and in midges (Downes, 1955) that the males first formed the swarm and the females entered the swarm later. Roth believed that the entrance of female mosquitoes was due to an acoustic response, while Downes was less committal. If such a male-female sequence existed in the present study it was not detected. But mating pairs have been observed dropping out of a swarm and onto the board. An observation was made on the relation between the size of the swarm and the frequency of such incidences. The swarms over boards of different sizes were observed for dropping out of mating pairs. The total number of pairs dropped out during a 5-minute period following the first pair was recorded. Only one set of records was obtained. The results (Table III) appeared to indicate certain trends.

The limited results indicate (1) that both sexes appeared in the swarm, (2) that there was a direct relationship between the size of the swarm and the frequency of mating pairs dropping out, and (3) that there is a minimun size of swarm below which no mating pairs dropped out. These facts suggest (*a*) that swarming facilitated mating, and (*b*) that chance collision might have played a major role in the mating of this insect.

Table III. The Size of the Swarm and the Frequency of Dropping out of Mating Pairs.

Board size	Number of midges in the swarm	Number of pairs dropped out
3 × 4 in.	4	0
4 × 6 in.	8	0
6 × 8 in.	14	5
8 × 12 in.	19	5

Swarming Over Two Boards

In order to study the relative attractiveness to the midges of two boards presented simultaneously, observations were made with two boards of the same size or of different sizes, and in two different arrangements. One arrangement involved placing the two boards side by side in relation to the direction of the sun (Fig. 3). This

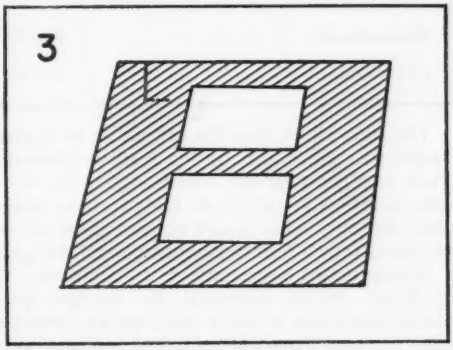


Fig. 3. Two boards arranged side by side. Other legends same as in Fig. 1.

was done by casting a shadow of an upright object and aligning the boards so that the front edges of both boards were in a straight line and were perpendicular to the shadow. This care was taken to ensure that neither board was favoured. The other arrangement involved one board behind the other in relation to the sun. Alignment was again aided by shadow casting.

Study No. 9. Swarming over two boards of the same size. When two 4×6-inch boards placed 1 inch apart were present, two definite swarms were formed, one over each board. When the boards were placed side by side, the swarms over the two boards were of the same size. When one board was placed behind the other,

there were twice as many midges over the front board as over the board behind. The former phenomenon has been observed by Gibson (1945) in *Spaniotoma minima*. He moved a sheet of black paper across a white background over which a swarm has been formed. When the black paper was at the centre leaving a strip of white paper at either end, the swarm divided, and about half the flies danced over each of the exposed white areas.

Study No. 10. Swarming over two boards of different sizes (arranged side by side). Two boards of different sizes were placed side by side at 1 inch apart. The distribution of midges as observed in close sequence and under the same conditions is given in Table IV.

Table IV. Number of Midges above each Board, when Two Boards were Placed Side by Side.

Board size	3 × 4	4 × 6	8 × 12
Observation a	4—6	10—14	
Observation b	0—1		15—20
Observation c		3—5	12—15

The data show that the attraction of a given board was influenced by the relative attraction from another near-by board. Thus, the 4×6-inch board attracted 10-14 midges when placed alongside a smaller board (observation a), but attracted only 3-5 midges when placed alongside a bigger board (observation c). Similarly, the 3×4-inch board attracted 4-6 midges when placed alongside a board twice as big (observation a), but attracted only 0-1 midges when placed alongside a board 8 times as big (observation b).

Study No. 11. Swarming over two boards of different sizes, arranged one behind the other. An additional observation was made with a 4×6-inch board and an 8×12-inch board. In this observation, the 4×6-inch board was placed in front of the other in relation to the direction of the sun's rays. The observation was made on a different day as the three observations in Study No. 10. The distribution of midges over the two boards is given in Table V.

The above comparison shows that while the swarms showed a ratio of 3 or 4 to 1 in favour of the larger board when the boards were placed side by side, the ratio was only 2 to 1 when the large board was placed behind the small board. This is in agreement with the results of Study 9, namely, that the position of the board played an important role in the distribution of midges.

Table V. Number of Midges Above Each of Two Boards, in Two Different Arrangements.

Board size	4 × 6	8 × 12
Boards side by side*	3—5	12—15
4 × 6-inch board in the front	8—10	15—12

* Observation c in Table 4.

Conclusions

Observations of the swarming behaviour of the midge (*Anarete near felti* Pritchard) revealed some interesting relationships between the size of the swarm and certain characteristics of the source of attraction. While some data were presented in numerical form, the results have more qualitative than quantitative significance in establishing certain trends.

The definite points revealed are as follows:

1. The midge was attracted to white surfaces particularly against a dark background. The attraction was directly related to the size of the white surface and the general light intensity. This was reflected by the relative speed of gathering of midges and the maximum number of individuals in the swarms. With a certain light intensity, there seemed a minimum size of the surface below which no midge was attracted.

2. The midge swarmed along the edges of a white surface which are nearest the sun. This was true whether the sun changed its position or the surface changed its orientation to the sun.

From the above facts, it may be suggested that the midges were attracted initially by a white surface in their vicinity. The midges then were attracted to a location where the contrast in lighting was the greatest.

3. In calm air, the midges faced the sun during swarming. They turned toward the wind when they were forced by the latter to alight.

4. The frequency of mating pairs dropping out of the swarm was in direct relation to the size of the swarm. It was suggested that chance collision played a significant role in the mating behaviour of this insect. It may further be suggested that swarming facilitated mating.

5. The attraction of a given surface to midges was influenced by the proximity and intensity of other attracting forces.

Acknowledgments

My sincere gratitude is due to Dr. A. Earl Pritchard, University of California, who kindly identified the species involved in the study.

REFERENCES

Cambournac, F. J. C. & Hill, R. B. (1940). Observation on the swarming of *Anopheles maculipennis* var. *atroparvus*. *Amer. J. trop. Med.*, **20**, 133-140.

Chapman, J. A. (1957). A further consideration of summit ant swarms. *Canad. Ent.*, **89**, 389-395.

Dodge, H. R. & Seago, J. M. (1954). Sarcophagidae and other Diptera taken by trap and net on Georgia mountain summits in 1952. *Ecology*, **35**, 50-59.

Downes, J. A. (1955). Observations on the swarming flight and mating of Culicoides. *Trans. roy. ent. Soc., London*, **106**, 213-236.

Fontaine, R. E., Green, D. H. & Smith, L. M. (1957). Ecological observations of the valley black gnat. *Lepoconops torrens* Townsend. *J. Econ. Ent.*, **50**, 764-767.

Frohne, W. C. (1953). A factor influencing male mosquito and midge swarms. *Mosquito News*, **13**, 27.

Gibson, N. H. E. (1945). On the mating swarms of certain Chironomidae (Diptera). *Trans. roy. ent. Soc., London*, **95**, 263-294.

Merritt, J. R. (1952). Butterflies and hilltops. *Lepid. News*, **6**, 101-102.

Roth, L. M. (1948). A study of mosquito behavior. An experimental laboratory study of sexual behavior of *Aedes aegypti* (L.). *Amer. Midland Naturalist*, **40**, 265-352.

Schneider, F. (1952). Untersuchungen uber die optische Orientierung der Maikafer (*Melolontha vulgaris* F. U. *M. hippocastani* F.) sowie uber die Entstehung von Schwarmbahnen und Befallskonzentrationen. *Mittl. Schweiz. ent. Ges.*, **25**, 269-340.

Snow, W. E. & Pickard, Eugene (1959). Localized effects of human hosts on the mosquito, *Mansonia perturbans*. *Ann. ent. Soc. Amer.*, **52**, 236-239.

Accepted for publication 31*st August*, 1960.

BEHAVIOUR OF THE LARVAE OF *Arrenurus fissicornis* Marshall, A WATER MITE PARASITIC ON DRAGONFLIES

By RODGER MITCHELL

Department of Biology, University of Florida

It has been argued that the well known tendency of larval water mites of the genus *Arrenurus* to attach to specific sites on their odonate hosts (Münchberg, 1935, *et seq.*) is related to the way in which the larvae re-enter the water after feeding on their host (Mitchell, 1959). The attachment of mites to their hosts is non-random, so some mechanism must limit the mites to particular sites. This study deals with that mechanism and with the sequence of events during a mite's larval life. A single species, *Arrenurus fissicornis* Marshall, is considered but other observations, that will be published in a comparative study, indicate the behaviour described below to be typical of many species assigned to the subgenus *Arrenurus*.

All the field work was done on the Edwin S. George Reserve of the University of Michigan, located near Pinckney, Michigan. The various officers of the Reserve have given me a very wide measure of support in the form of Grants-In-Aid from the Edwin S. George Scholarship Fund while permitting the greatest freedom in research.

Introduction

Arrenurus fissicornis is a member of the subgenus *Arrenurus*. Through an extensive series of rearings (see Münchberg, 1959, for citations to most of this work), it is known that larvae of this subgenus are typically parasitic on dragonflies. The life cycle of all known *Arrenurus* species follows the basic water mite pattern with the first stage, the larva, parasitic on an insect imago; this is followed by two stages, the nymph and the adult, which prey on microcrustacea. To date the date on life cycles of *Arrenurus* species are based on rearings of engorged larvae from field collected hosts. The larvae are removed from the host and reared through subsequent stages in the laboratory.

Such studies commence after larvae complete their period of greatest activity, and nothing worthy of note has been seen in the behaviour of the nymph and adult under these circumstances. Engorged larvae exhibit some reactions which have been considered recently. Engorged larvae may be thin-skinned and respond to moistening or they may develop a thick skin and be entirely unresponsive. Thick-skinned larvae are usually on the thorax of the host; thin skinned larvae are usually on the last abdominal segments. It was concluded from these data that some parasites have adaptations for leaving the host when it oviposits and these are the thin-skinned, responsive larvae. Larvae of other species ride on their host until its death, which must occur in or over water if the parasites are to re-enter the water (Mitchell, 1959). This work demonstrated that the larval attachment site on the host was one of the important adaptations related to the way the larvae re-enter the aquatic habitat.

Larvae attach to their host when the host imago emerges from the naiad skin. Thus attachment occurs within a narrow span of time and can be observed rather easily. The observations reported below deal with the parasitism of *Libellula luctuosa* Burm. and *Erythemis simplicollis* (Say), by *Arrenurus fissicornis*. This mite attaches to the terminal segments of the abdomen and drops from the host at the time of oviposition or pseudo-oviposition (Mitchell, 1959). Unengorged larvae cannot be specifically identified or reared through, but reliable presumptive associations could be made because all observations were made at one pond (Burt Pond) where long term studies had shown *A. fissicornis* to be the only common parasite of the above hosts.

Host Emergence and Normal Activity of the Mite Larvae

If terminal naiads of either odonate host are collected in the pond or just as they leave the water, they are often found to have clusters of mite larvae on the posterior surface of the head or on the anterior surface of the prothorax. The mite clusters are generally very assymetrical unless the larvae are so numerous as to compete for resting sites. The larvae are inactive and attached to their mouthparts, but the larvae do not appear to be feeding on the naiad.

On leaving the water the naiad climbs some object and there the imago emerges from the old skin. The skin first splits forward along the middorsal line from the base of the forewings to the anterior margin of the thorax. The split then extends over the head and, at a central position, divides into two lateral splits extending down

over the eyes. The imago expands its bulk while the naiad skin splits and, after the splitting of the skin is complete, movements of the imago raise it dorsally out of the old skin. Once the head and thorax are free, the abdomen is moved so that the imago rises upward through the split in the naiad skin. In order to tabulate the data conveniently, the time from the beginning of the split to the completion of the split is designated 'Stage I'. As the imago moves out of the skin it is said to be in 'Stage II'. When only a few terminal segments of the abdomen remain in the naiad skin the imago ceases all activity for a period of time and this period of inactivity is designated 'Stage III'. At the end of this stage the imago crawls free of the old skin.

Larvae on the host naiad are not easily disturbed, and even if the host spends considerable time searching out a site for emergence there is no activity among the larvae. The larvae even remain quiet, except for the twitching of a few legs, for a period of five to six minutes after the naiad skin splits and host emergence begins. By this time the imago has been free of the skin where the larvae are situated for at least two or three minutes and only the posterior of the abdomen is in contact with the naiad skin.

Data on the timing of the events during host emergence are given in Table I. If the times of stages are compared with the time of mite activity, it is seen that mite activity is not coordinated with any particular physical event of emergence; but it is clear that mite activity always begins after the head and thorax of the imago are free of the nymphal skin. In Fig. 1 the various events during an emergence are graphed. The part of the host that will be contacted by a mite larva crawling from the nymphal skin to the imago at various times during emergence is indicated by the shaded areas. All these data show that the membranes to which mite larvae normally attach are on the part of the host that the larvae strike when they first crawl on to the imago. Hence, there is no necessary reason to postulate any attachment site recognition on the part of the larvae.

The Movement of Larval Mites on to the Host Imago

Clusters of larval mites on the posterior surface of the head or on the anterior face of the thorax of the host tend to be near the mid-dorsal line with the larger clusters extending furthest down the lateral surface. When the larvae become active during the emergence of the host, a few of the peripherally placed mites may wander

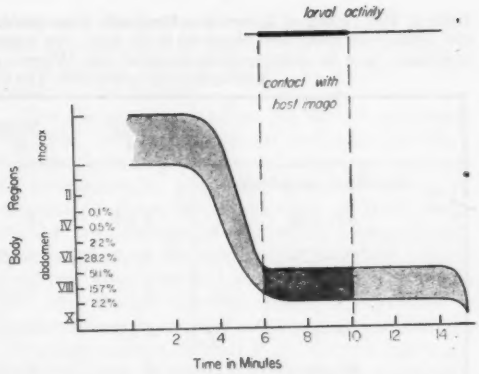


Fig. 1. A graphic representation of the events during the emergence of an adult *Erythemis simplicicollis* and the coordinated activity of the mite larvae. The shaded area is an approximate indication of the parts of the host that will be contacted by a larva crawling from the naiad skin at the various times during emergence. The numbers along the ordinate give the percentage of the mite larvae attached to the various abdominal segments in a sample of 14 *E. simplicicollis* collected on June 20th, and 21st, 1959. The graph is based on observation 59-13.

about in most any direction, but the majority of the cluster mill about in the same general area. Larvae that wander dorsally over the split and touch the inner surface of the naiad skin never return to the cluster. Consequently, the cluster appears to move dorsally even though there is no clear orientated movement of individual larvae toward the split. This loss of larvae in one direction is the simplest explanation for the apparent movement of clusters dorsally.

When a larva is inside the naiad skin it is virtually certain to contact the host imago in its wanderings. There does not appear to be a specific stimulus attracting the larvae to the host imago, but the larvae do seem to recognize the imaginal integument by touch for they begin to probe for attachment sites with their mouthparts as soon as the imago is touched. No larva was ever seen to leave the host.

When there are very few mites the larvae unload from the naiad to the imago very slowly and have less success in finding the imago. Only a few such cases were observed and more data must be collected, but it appears that if there are fewer than fifty larvae the unloading is quite inefficient. It is as if an unloading pressure resulted from many individual kineses acting together. When too few mites are present the weak individual kineses may prove to be inadequate.

Table I. The Timing of Events in a Dragonfly Emergence. All records were taken between May 31st and June 7th (1959 and 1960) from specimens observed in the field. The stages are arbitrary divisions defined in the text and the time is given in *minutes since the splitting of the nymphal skin*. Where a question mark is entered the time of splitting was not accurately known but was estimated. The time of the end of the stage is given.

	Stage I	Stage II	Stage III	1st mite activity	1st host contact	All mites on host
Erythemis simplicicollis						
59—12a	4 1/2	8	24 1/2	—	—	—
59—12b	3	5 1/2	19	—	—	—
59—12c	3	5 1/2	24 1/2	—	—	—
60—45	4 1/2	8 1/2	24 1/2	—	—	—
60—64	4	8 1/2	23	—	—	—
60—58	3	6	20	—	—	—
59—11	2	5	20	6	7	9
59—12	4	7	23	5	—	13
59—13	3	6	15 1/2	5 1/2	6	—
59—14	4	6 1/2	—	5 1/2	7 1/2	10 1/2
59—15	4	6	—	5 1/2	6	11
59—16	4(?)	6 1/2	22 1/2	6	8 1/2	11 1/2
59—26	4 1/2	8 1/2	17 1/2	6 1/2	—	—
59—56	5	9	28	5 1/2	7 1/2	—
Libellula luctuosa						
59—07	2 1/2	6 1/2	22 1/2	—	—	—
59—24	5 1/2	9 1/2	34 1/2	—	—	—
59—25	4 1/2	9	25	9	12	—
59—27	4	7	—	—	—	—
59—30	4(?)	7 1/2	27 1/2	9	10 1/2	14 1/2
59—31	4(?)	7 1/2	25	7	7 1/2	12 1/2

Locomotor Responses of the Larvae

Two kinds of locomotor activity can be elicited from larval mites: the slow milling about of larvae that is seen during host emergence or when larvae on the naiad are disturbed, and a rapid swarming response which results in larvae swimming from the naiad, if the host is in water. This reaction can be seen only if a naiad is wounded or damaged and the advantage of such a response is obvious. The stimulus for this reaction is unknown.

In order to test for the various reactions during emergence, the exact time the naiad skin began to split was carefully noted. Then at various intervals the mid-dorsal line of the emerging imago was pierced with a tiny hooked scalpel which was moved about so as to destroy the thoracic tracheal sacs. This stopped all movements of the emerging dragonfly. All the experiments were done on *E. simplicicollis* naiads bearing a heavy load of mites.

Four hosts were damaged either before emergence or within 15 seconds of the time the naiad skin had split and the mites on these hosts showed a rapid locomotor response within 60 seconds of the wounding. When 30 or more seconds of emerging time had elapsed the larvae on the

wounded host generally remained quiescent until about the normal activity time. In 9 experiments the wounding was done 30 to 800 seconds after skin splitting; 7 experiments showed normal slow activity of the larvae 210 to 330 seconds after skin splitting of the host (mean 270). This is slightly earlier than normal activity time (300 to 390 seconds after skin splitting) but it is an activity more closely correlated with the beginning of host emergence than with the wounding for the interval between wounding and larval activity varied from 30 to 295 seconds (mean 164).

Thus it appears that normal larval activity will not be shown unless some 30 seconds of emerging time have elapsed and that a stimulus during this time sets off a series of larval responses that cannot be altered by subsequent manipulation.

Two exceptional experiments were eliminated from the above discussion as due to mishandling or some unrelated phenomena. One wounding at 30 seconds resulted in slow larval activity 120 seconds after splitting and a wounding at 90 seconds resulted in slow larval activity 750 seconds later. A second case of extreme delay in larval activation was noted when no manipulation was involved; a *Libellula luctuosa* took nearly twice the normal time to complete Stage I and in this case the activation of the larvae was delayed an equal amount. Perhaps the stimulus affecting activity of the larvae is normally produced over a brief period of time but under some circumstances the stimulus is modified so as to lengthen the period of larval quiescence.

Mites clustered on a terminal naiad can be stimulated to activity if forcibly detached but as long as the larvae are in contact with the naiad they show a slow crawling response and will shortly reattach themselves to the naiad. The general mode of locomotion when disturbed but still in contact with the host is similar to the slow activity during emergence, and these may be identical responses that can be elicited under different circumstances.

Attachment of Larvae to the Host Imago

Because of the delay in activation the larvae always contact the host abdomen when they first leave the naiad skin and very shortly attach to a nearby membrane. If mite larvae are transferred from the abdomen to the thorax there seems to be no difference in behaviour. Larvae continue to test the membranes with their mouth-parts and soon attach to a thoracic membrane. Evidently there is no discrimination of membranes on the part of the larvae. The hosts cannot be kept in confinement and it is not known whether normal development will ensue on the thorax.

The number of parasites per host is extremely variable, but if imagos are collected as they emerge there is a certain constancy in the level of parasitism at a specific location. Seven *E. simplicollis* from the north side of Burt Pond carried an average of 3·2 mites (range 0-16); nine hosts from the south side (less than a hundred feet away) carried an average of 54·2 mites per host (range 13-100). There is doubtless a random introduction of engorged larvae around the entire margin of Burt Pond for the hosts are not restricted in their activity nor is there any distinct localization of the mite adults in the pond. Perhaps the explanation for non-randomness of larval parasitism will be found in the differential success of either eggs or larvae in certain situations.

Discussion

It is now possible to outline the sequence of events in the parsitism of a libelluline host by *Arrenurus fissicornis*. All of the larval activities observed to date have been taken into account. The precise stimuli perceived by the larvae are unknown, but various experiments fix the circumstances existing at the time of the responses and show that there is a defined sequence of events. The data on experiments and observations have been given and in the following paragraphs the conclusions are put together in summary form.

Nothing is known about the various elements involved in the 'searching activity' of newly hatched larvae. In the laboratory this appears to be an incessant activity that is not modified in the presence of a host naiad. It may only be a mode of locomotion involving no distance perception of the host. Larvae cease swimming on contact with the host and quickly come to rest on the host nymph. Local differences in the level of host parasitism could be the result of a searching activity that is efficient in bringing about parasite-host contacts under a limited set of circumstances. Local variation in the rate of parasitism would result from this unless the hosts were in situations where parasite searching activity was uniformly successful.

The stimulus eliciting larval quiescence on the host is specific for healthy last instar naiads and may be increasingly effective as last instar naiads mature. Cast skins, naiads with unrepaired wounds, and early instars do not evoke a

response. But a variety of hosts may be accepted by the larvae in the field so it is probable that some general property of healthy terminal naiads is perceived by the larvae at the time of host contact.

Once the larva is on the host it remains quiet unless disturbed by abrasion or host grooming. Such disturbances are quite frequent on all surfaces except the deep cervical groove between the head and thorax. Clusters of larvae may come to lie on the protected cervical and thoracic surfaces because they are constantly disturbed until, by chance, they enter the groove between the head and thorax. Larval clusters are dorsally placed and this may be the result of a specific orienting behaviour. When there are less than 150 larvae on a naiad the clusters are almost always assymetrical. This too may be the consequence of a random selection of the four undisturbed areas (the right or left sides of the posterior of the head or the anterior of the prothorax) by the first larva to attach and a tendency of other larvae to cluster around a quiescent larva. Precise data on larval clusters could not be collected without interfering with subsequent observations and these reflections stand as unverified speculations.

The second response of quiescent host-attached larvae is elicited by damage to the host (i.e. wounding) and body fluids escaping from the wounded host could provide the stimulus. The mite reaction is a prompt resumption of what appears to be normal 'searching activity'.

This abandoning of the host can be elicited in quiescent larvae up until about 30 seconds after splitting of the naiad skin during normal emergence of the imago. From that time on neither disturbance nor wounding of the host can break larval quiescence or modify the subsequent chain of behaviour.

There is no evidence as to what the 'emergence stimulus' may be. Apparently there is some quantitative relationship between the stimulus and the length of quiescence. Normally the larvae are quiescent for four to five minutes after the emergence stimulus and then begin slow movements that tend to bring them into contact with the host imago. These events have been discussed in detail and it was concluded that: (1) timing of larval activity, not specific site recognition, explain the non-random attachment of larvae to the host, (2) discovery of the imago involves no distance perception, and (3) imagos are recognised only through touch.

Once attached to the imago the larvae feed and engorge. There is no thickening of the larval cuticle and engorged larvae can be stimulated to slow activity by moistening. As discussed elsewhere (Mitchell, 1959) this response results in the larvae tending to drop in the water during host oviposition. The libelluline hosts involved dip their abdomens into the water when ovipositing and the males of *L. luctuosa* regularly pseudo-oviposit (Jacobs, 1955). When the larva is back in the water it transforms into the quiescent nymphochrysalis stage from which the nymph will emerge.

Summary

Larvae of *Arrenurus fissicornis* become active and move on to the emerging dragonfly host only after five minutes of emerging time has elapsed and the membranes they must encounter first are those of the terminal abdominal segments. Larvae attach to these membranes. If the emergence of the host is stopped (by manipulation) thirty seconds or more after host emergence begins the entire sequence of normal mite activity is unaltered; earlier manipulation causes larvae to abandon the host. Larvae will attach to any host membrane they are placed upon. Thus, it appears that timing alone is responsible for site specificity and that the stimulus evoking the behaviour of mite larva during host emergence is perceived during the first thirty seconds of host emergence.

The lack of strong orientation among larva before they encounter the naiad, when they cluster on the cervical membranes of the naiad, or when they transfer from the naiad to the imago suggest that distance perception is not involved. Random movements and touch perception can adequately explain most of the observed behaviour of the mite larvae.

Acknowledgment

I offer this as a token of my appreciation for the wise counsel Irving J. Cantrall has lavished on me during his tenure as Curator of the George Reserve.

REFERENCES

Jacobs, M. E. (1955). Studies on territorialism and sexual selection in dragonflies. *Ecology*, **36**, 566-586.

Mitchell, Rodger (1959). Life histories and larval behavior of arrenurid water-mites parasitizing Odonata. *J. N.Y. ent. Soc.*, **67**, 1-12.

Münchberg, Paul (1935). Zur kenntnis der odonatenparasiten, mit ganz besonderer Berüchsichtigung der Ökologie der in Europa an Libellen schmarotzenden Wassermilben-Larven. *Arch. Hydrobiol.*, **29**, 1-120.

Münchberg, Paul (1959). Dritter beitrag über die an africanischen Libellen schmarotzenden *Arrenurus*-Larven (Hydrachnellae, Acari). *Arch. Hydrobiol.*, **55**, 264-275.

Accepted for publication 6th December, 1960.

BRIEF COMMUNICATION

A RESPONSE OF THE ALBINO RAT TO RED LIGHT

By A. P. MEAD*

Department of Zoology, University College of Ghana

It is useful to observe the behaviour of rats through a screen, the principal quality of which is that the rat does not see the experimenter.

It has long been assumed that the vision of most rodents is poor towards the red end of the spectrum, because of the small cone representation in the retina (Watson & Watson, 1913). The work of Coleman & Hamilton (1933), Munn & Collins (1936) and especially Walton & Bornemeier (1938) has, however, shown that the laboratory rat can perceive red in some experiments in which it was presented in combination with other colours. There is still, however, some doubt about the exact visual sensitivity of the rat in the red.

The method devised by Mead (1960) suggested the possibility of finding out by observation of its exploratory behaviour whether red light in a restricted wave band was visible to the rat. For this test a Wratten filter No. 70 A (passing light of wave-length not less than 6,500 Å) was chosen as the light is just visible to man. This filter might have proved useful as an observation panel if it could be shown that the rat could not perceive the light it transmitted.

Method

The experiments were performed in a laboratory consisting of two small rooms with a communicating door. One room was used as an experimental room and the other for observation. A square of hardboard of size four feet was placed in the experimental room supported to a height of fifteen inches from the ground. The room was completely blacked out. A 60 watt pearl bulb was arranged in a light proof box with the Wratten filter under it. This was than screened so that the light passing through the filter illuminated half of the square. There was no other light in the room other than that thrown directly on to the square through the filter and that reflected from the illuminated part of the square.

The movements of the rat in the red illuminated half of the square were observed through a contrast observation panel (Mead, 1960). The observation room was also completely blacked out. When a rat moved into the dark half of the square it was not visible to the observer.

The rats used in this experiment were Wistar albino males of weight range 200-300 grammes. They were socially and environmentally disturbed (Mead, 1960) for five days before the test. This was previously found to cause an increase in exploratory activity. On the day of the test each rat was dark-adapted for a period of twenty minutes before the experiment was started. The cages were placed inside a light proof box which had been painted inside with matt blackboard paint.

Eight rats were tested by placing them on the square on the border between the red illuminated and dark halves. Each was placed in the centre of the board. They were also placed facing alternately in opposite directions to prevent directional bias at the start of the test. After each test the square was wiped over with a damp cloth and then was left to dry. The faecal pellets were removed and the urine spread as evenly as possible. This precaution was taken to reduce the possibility that scent would be left as a directional cue on the square.

The first eight results appeared conclusive but were open to two criticisms:

(i) The first rat may have fortuitously spent more time in the dark half and the other seven were following its scent in the absence of other cues despite the precautions taken.

(ii) The rats were all moving away from the door through which the observer returns. This would tend to place them in the dark half.

Previous observations (Mead, 1960) had shown that the second criticism was not valid. In an illuminated open square experiment in which the rats could clearly see in which direction the observer returned no effect of this kind was observed. Sixty-four rats showed directional tendencies only in relation to discontinuities peripheral to the square; these, in thirty-two rats, were in the same direction as the door containing the observation panel.

The possibility that trail following would occur in a situation in which the cues were absent had been greatly reduced by the precautions taken.

*This work was performed during the tenure of a research scholarship in the Department of Pharmacology, University of Birmingham.

However another eight rats were used in a further set of tests. In this, the square was turned so that the half which was previously in darkness was now in the red light. If trail following was occurring it should now produce opposite effects from that previously obtained.

Result

The result is summarized in Table I. The first eight rats spent more time in the area not illuminated.

Table I.

Male albino rats 200-300 g.	Mean time in Red light. (seconds)	Mean time in darkness. (seconds)
Rats no. 1-8	86·25	213·79
Rats no. 9-16	85·63	214·37
Rats no. 1-16	85·93	214·07

The next eight rats also spent more time in the area not illuminated. This showed that the rats were affected by the illumination and were not trail following. Had scent been the stimulus causing the result in the first set then in the second the rats should have spent more time in the red illuminated area in which there would have been a greater scent accumulation. The results were, however, closely similar for all the rats in both groups of the tests. Had scent been a factor influencing the movement then the mean of the second set of eight rats would have been different from that of the first set. This was not so. This is evidence in favour of a single factor orientating the result, namely the differential illumination.

Combining the results for all sixteen rats also showed the same effect.

All these differences are statistically significant and are below the 5 per cent. probability level.

Conclusions

It is concluded that rats used in this test could perceive light of 6500 Å wave-length.

These rats reacted to the differential illumination in the same way as rats differentially illuminated by normal electric light. This is shown by comparing this result with that found in earlier work (Mead, 1960). It was then shown that rats spend more time exploring in the less well illuminated section of a similar area differentially illuminated.

It is also suggested that this method would prove useful in the investigation of similar problems of sensory discrimination.

REFERENCES

Coleman, T. B. & Hamilton, W. F. (1933). Colour-blindness in the rat. *J. comp. Psychol.*, **15**, 177-181.

Mead, A. P. (1960). A quantitative method for the analysis of exploratory behaviour in the rat. *J. anim. Behav.*, **8**, 19-31.

Munn, N. & Collins, Marjorie (1936). Discrimination of red by white rats. *J. genet. Psychol.*, **48**, 72-87.

Walton, W. E. & Bornemeier, R. W. (1938). Further evidence for colour discrimination in rodents. *J. genet. Psychol.*, **52**, 165-181.

Waton, John B & Watson, M.I. (1913). A study of the response of rodents to monochromatic light, *J. anim. Behav.*, **3**, 1-14.

Accepted for publication 3rd August, 1959.

PROCEEDINGS OF THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

A symposium on "Orientation and Migration" was held on Tuesday, 11th July, Wednesday, 12th July, and Thursday, 13th July, in the Department of Zoology, Cambridge University, by kind permission of Professor C. F. Pantin, F.R.S. The programme was arranged in collaboration with Dr. J. D. Carthy, and the President, Dr. K. Mellanby, C.B.E., took the chair.

PRESIDENTIAL ADDRESS: EFFECTS OF TEMPERATURE AND HUMIDITY ON THE BEHAVIOUR OF POIKILOTHERMS. By K. MELLANBY.

All animals are affected by the temperature and humidity of their surroundings, and these conditions often modify behaviour. Warm blooded mammals and birds may only complete more or less complicated patterns of behaviour over a restricted range of temperature, and if it is hotter or colder they may behave "abnormally." The effect, particularly of temperature, on cold-blooded animals is, however, even more fundamental. When cooled sufficiently all poikilotherms go into "chill coma"; this occurs some degrees above the temperature where death from cold takes place. The temperature causing cold anaesthesia differs for different species of animals, and is not always the same for the same species. We may say that a warm blooded animal does not do something when it is cold because it does not like doing so; the cold blooded animal in chill coma is immobile and is therefore quite unable, physically, to perform at all!

When a cold-blooded animal, in chill coma, is warmed gradually, it recovers and may start to move. The first movements are sluggish and unco-ordinated. As the temperature rises the animal becomes more active—or at least capable of greater activity. Many insects will crawl at a fairly constant speed if placed on a suitable surface on the laboratory bench, and the rate of crawling in relation to temperature may be expressed on a graph. The result is often a more-or-less hyperbolic curve, similar to that obtained when the rate of metabolism, or the rate of development, of many poikilothermous animals is studied over a range of temperature.

However, animals seldom behave all the time as though they were automata dependant entirely for their activity on their body temperature, as do non-moving stages such as eggs, insect pupae, or even experimental insects like the fasting mealworm which do not move appreciably during an experiment. It is the behaviour of the animals, the results of their reactions to stimuli either from outside in the environment or internal stimuli from within the animals themselves, which cause them to differ so fundamentally from these non-moving stages.

The position of the chill coma temperature, below which movement is impossible, is probably the most fundamental point in the life of a poikilotherm. Contrary to common belief, the position of the chill coma temperature in many species is not rigidly fixed, but may be surprisingly easily and rapidly altered. In insects and amphibia acclimatization (or, as some prefer, "acclimation") often may be complete in under 24 hours. Thus the larva of the yellow fever mosquito, *Aedes aegypti* kept in a culture at 34° C. has a chill coma temperature of 10·80° C., larvae from this same culture kept overnight at 17°C. have a chill coma temperature of 5·7°C., and after exposure of 12 hours to 10°C. the chill coma temperature is reduced to 3·4°C. This process is reversible, and the same larva can have its chill coma temperature altered, either upwards or downwards, many times. Frogs and salamanders behave similarly to insects. Acclimatisation is well-known, though perhaps slower, in fish. Somewhat surprisingly acclimatization does not seem to operate in slugs.

There sometimes seems to be a contradiction between the results of laboratory experiments to determine the lowest temperature where movement can occur, and field observations on when spontaneous movement does, in fact, begin. The chill coma temperature may be many degrees below the temperature at which spontaneous activity seems to begin, and there may be quite a wide zone of temperature where movement is possible but where it seldom, if ever, occurs. Much more work on the physiology and activity of animals in this zone is needed. We need to distinguish between different kinds of stimuli which may cause activity. Some stimuli arise

within the animals, and to the observer these produce "spontaneous" movements; others, including changes in temperature, humidity or light, and even such crude operations as poking the animal with a stick, are clearly external. It is easy to demonstrate that a stronger external stimulus is needed to produce a reaction just above the chill coma temperature than when it is a few degrees warmer, for a gentle touch with a needle at $x + 5$°C. will be as effective as a severe jab at $x + 1$°C. The exhaustion of food reserves, producing hunger, could be considered as an internal stimulus, and there is some evidence that reserves have to be more completely exhausted to stimulate some animals to seek food at low temperatures than at high, where the lesser stimulus may be effective. This distinction between external and internal stimuli is somewhat artificial, as they are often interrelated; for instance a hungry animal under certain conditions may remain motionless and may not spontaneously seek for food, but it may be more easily excited by an external stimulus than an animal with good food reserves.

There is no doubt that in many cold-blooded animals the position of the chill coma temperature can, easily and rapidly, be altered several degrees centigrade. There is some doubt as to whether the position of the temperature above which spontaneous movement, and normal activity, occurs is so readily altered, or even whether it can, in some cases, be altered at all. I think that, at any rate with crawling and swimming insects, there is evidence that the threshold temperature for spontaneous activity moves parallel with the chill coma temperature, but more field and laboratory observations are required.

The results of some further experiments with yellow fever mosquito larvae are worth considering in this connection. I have already explained how acclimatization may alter the chill coma temperature from 10·8°C. to 3·4°C. At a temperature of only 1°C. above the chill coma temperature, whatever that may be, the larvae appear normal, they swim and wriggle spontaneously and respond readily when prodded with a needle. However, some reactions do not appear until about 5°C. above the chill coma point. This may be easily demonstrated for the "alarm reaction". If a dish containing *Aedes aegypti* larvae at, say, 20°C. is tapped with the finger, or if a hand is moved over the surface to cast a shadow, the larvae immediately swim actively down from the surface and remain at the bottom of the dish for about 4 minutes. However, larvae acclimatized to 10°C., with a chill coma point of 3·4°C. do not give any alarm reaction at all until the temperature passes 9·5°C.; between 3·4°C. and this temperature they were otherwise normal and active. The threshold for the alarm reaction of larvae acclimatised to 17°C. (chill coma temperature 5·7°C.) was 11·0°C., and for those acclimatized to 34°C. (chill coma temperature 10·5°C.) was 14·3°C. Now the alarm reaction is, of course, a reaction to an external stimulus, but it is a reaction to a type of stimulus which frequently operates in nature, and is of rather a different nature to that produced by prodding with a needle. It is interesting also to note that with a rising temperature the alarm reaction was suddenly restored; larvae acclimatized to 34°C. gave no reaction to a shadow at 14°C., but at 14·5°C. every individual in the culture seemed to respond. It appears then that different stimuli may have different temperature thresholds. It also seems that the position of these different thresholds may be considerably altered by acclimatization.

There is a good deal of laboratory evidence, and some from the field, that a change in temperature, within the zone of normal activity, may produce activity in an animal which would move little or not at all in a constant temperature. Thus as my colleague Mr. R. A. French and I described to this Society, larvae of the mealworm *Tenebrio molitor* will go into a state of apparent coma if placed for an hour in glass tubes, and if they are carefully tipped onto the surface of a dish of bran they will not burrow immediately but will lie on the surface for a considerable period so long as the temperature does not fluctuate. If the temperature is raised or lowered as rapidly as 1°C. in 5 minutes, the larvae soon become active and burrow. Slugs of several species, if kept in dishes in the laboratory at 15°-20°C., will usually be found contracted and motionless, even if the humidity is favourable (i.e. near to saturation). If the temperature is reduced to below 10°C. the slugs start crawling actively. It has been suggested that examples like these are at least partly explained by experiments in which increased action currents in the nerves of poikilotherms have been observed following changes in temperature. Other experiments have shown a transitory rise of metabolism when a poikilothermous animal has been cooled, though later the metabolism has usually fallen to the appropriate lower level.

There is no doubt some connection between these physiological phenomena and the effects of changing temperature on behaviours, but the results require careful interpretation. Movement under controlled laboratory conditions may have little relation to spontaneous and natural behaviour. The mealworm in the experiment described above does indeed move more actively when the temperature changes, but it moves eventually under constant conditions particularly if it is "hungry". A mealworm larva living in bran is surrounded by food. It only needs to move to feed, and can with advantage lie still for the rest of the time. Under favourable temperature conditions larvae grow as rapidly in constant temperatures as when the temperature fluctuates and when it might therefore be expected to cause additional activity which might be advantageous. The case of the slugs is even more striking. Experiments on activity have caused it to be suggested that unless the temperature is periodically reduced cultures will not thrive. My colleague, Mr. J. W. Stephenson, has found that if slugs are maintained with adequate food at a constant temperature of 20°C. (conditions which some have suggested would seriously inhibit activity) they grow many times more rapidly and successfully than they do at lower temperatures, though these might stimulate them to activity in the laboratory. At 10°C. they do not move about unnecessarily, but when they require to feed they do not hesitate to do so.

Adult insects with wings may crawl or fly. These two activities have certain fundamental differences. I have already pointed out that, just above the chill coma temperature, an insect may crawl very slowly, hardly moving at all. If the temperature is gradually raised the speed of crawling gradually increases, and the fastest speed of crawling may be a hundred times as great as the slowest. The threshold temperature for crawling may be many degrees below that at which efficient flight is possible. If a winged insect is dropped at a temperature just a little above the (crawling) chill coma temperature, it will probably drop down without moving its wings. If the temperature is raised a few degrees —conditions where active crawling is possible— on being dropped an insect may move its wings, but it may be unable to make height and will land at a lower level than it starts. Proper controlled flight is only possible at an even higher temperature. (I am not here considering the rather unusual cases of large moths which warm up their bodies—and their "engines"—by vigorously beating their wings on cool days). Now though some insects, like dragonflies and syrphids, are capable of flying at a wide range of speeds, the majority of insects, particularly of those making up the aerial plankton, have only a narrow range of speeds of flight, so that their maximum speed is little higher than their "stalling" speed. Thus while the speed of crawling may increase over a wide range of temperature, and while this speed may be expressed, graphically, in a hyperbolic curve, flight is often an all or none process, and above the threshold any increase in temperature may have little effect on its speed.

Flight is seldom observed until the temperature of an insect is several degrees above the chill coma temperature, thus the tsetse fly, *Glossina palpalis*, may have a (crawling) chill coma temperature of 8°C., but spontaneous flight is seldom if ever seen below 20°C. I have no record of acclimatization affecting the flight threshold of an insect; it is possible that some different mechanism may control this process.

In recent years a great deal of work on diurnal rhythm has been done, particularly the distinguished studies on insects by Dr. Janet Harker in this University of Cambridge. We know that, under constant conditions in the laboratory, the endocrine system may play an important part in the control of diurnal rhythm. If insects which show diurnal rhythm are kept at temperatures anywhere within their zone of normal activity, the "clock" controlling their activity is not affected by changes in temperature and it keeps good time. However, if the insects are in chill coma the clock is stopped, and on regarding the insects the clock is "slow" and activity is delayed. Nevertheless, temperature changes within the normal zone can have other effects on insects which have diurnal rhythms.

Two such insects are the cockroach, *Blatta orientalis*, and the bedbug, *Cimex lectularius*. Some 20 years ago I found a natural infestation of both these insects in an animal house. I found that each night the cockroaches came out of hiding and ran actively around in the hours immediately after dusk; the bedbugs seldom appeared then, but were active shortly before dawn. There was, however, a fundamental difference between the two species of insects. The cockroaches came out, mainly to feed, every night. Bedbugs take a large blood-meal, which they take several days to digest, and they

did not come out again for at least three days after feeding. Their rhythm was not a 3-day one, for it seems that if a bug did not find food the first night it came out of hiding it was again active 24 hours later. Also the period between bouts of activity could be altered by changing the temperature—under cool conditions a bug digested slowly and lay dormant for 2 weeks or longer, under warm conditions it fed twice a week, but however long the period between feeds activity occurred during the last hours of the night.

The clocks controlling diurnal activities are therefore by no means all powerful. A cockroach, prevented from feeding at night at the time it "ought" (if it relies on its clock) to be active, perhaps by keeping the feeding area too brightly lit, will eat readily in the middle of the next day in a darkened arena. Hungry bedbugs placed on warm skin will feed at any time of night or day. However, studies of feeding behaviour under these conditions may give results which differ from those obtained under natural conditions when the normal interplay of external and internal stimuli is in operation.

We tend to underestimate the amount of time cold-blooded animals spend motionless. Bands of locusts may display almost constant activity for hours at a time, but most cold-blooded animals only move when they are seeking food, when they are actually feeding and when they are concerned with sex. For instance, caterpillars of the cabbage butterfly, *Pieris rapae*, go through an interesting rhythm. They usually feed on the edges of the leaves of their host plants for a few minutes only, after which they crawl to another part of the plant where they remain motionless for some hours, apparently "asleep". In cool conditions they feed more slowly and "sleep" for longer periods between meals than they do when it is warmer. The rhythm seems unaffected by changes in light and humidity, though mutual stimulation between members of a batch of caterpillars has its effects. If these larvae are disturbed between meals they can be made to perform various antics, but this behaviour may have little relation to that found in nature. I think that some of those who have studied the behaviour of poikilotherms have tended to forget that they are dealing with animals which are normally subject to a whole complex of external and internal stimuli, and that frequently in our experiments they are being made to be active when normally their normal reaction would be to curl up and sleep. Real progress in the study of the behaviour of poikilothermous animals will only be made when experiments are more closely related to the natural conditions under which the animals normally live, and when it is realized that their activity and behaviour has some purpose other than the education of the experimenter.

PRESENT TRENDS IN ORIENTATION AND MIGRATION STUDIES. By J. D. CARTHY, *Queen Mary College, London University.*

The characterization of a migratory animal is not simple. Though the criteria suggested by Kennedy (1961) apply to the insects he was considering, it cannot be generally stated that migratory animals show a reduction of vegetative behaviour. However migration is itself characteristically a movement in one direction for long periods. As it is becoming clear that much the same behavioural mechanisms are employed, it is important to consider the orientated movements of animals made at tidal, or daily, intervals, often for the purpose of feeding, when discussing the behavioural bases of migration. Two categories emerge from a consideration of these two behaviour patterns. First, the individual headings may be at random but the overall movement is in one direction. Second, each individual's path is directed in the same direction. The first is typical of aphids and locusts, and the second of migrating birds and of *Talitrus saltator*, *Velia currens* and other invertebrates. The straightening out of a tortuous path may have survival value in a search for optimal conditions. This can reasonably be called 'navigation' at least when sun or stars are the orientation points used. It need not be directed towards a goal, as it is not in *Velia* and in some birds at least (e.g. Mallards; Matthews, 1961).

The role of learning and exploratory behaviour in orientation and homing, particularly, in mammals, was briefly discussed.

THE LONGITUDINAL ORIENTATION OF LARVAL HONEY BEES (*Apis mellifera* L.) WITHIN CELLS. By S. C. JAY, *Rothamsted Experimental Station, Harpenden.*

Disorientated larvae of the 3 castes (worker, drone, queen) of honey bees rarely occur under natural conditions. When pupae were reversed in natural cells, only queens emerged, the other

castes dying. Correct orientation before metamorphosis is therefore essential for survival in the worker and drone castes.

The 3 castes are reared in distinctive cells that were simulated in the laboratory by gelatin capsules. The end walls of these were modified to give various combinations of shape, ventilation, and texture. The effect of cell length and gravity was also tested. Artificial capping materials (e.g. paper tissue ("Kleenex"), surgical gauze, gelatin capsule lids with fine inward punctured pin holes, fine mesh plastic screening) were successfully used under both natural and laboratory conditions.

Larvae of the 3 castes that were spinning cocoons were put in various artificial cells and their subsequent behaviour and orientation observed. The following was concluded:—

(1) Larvae have a sense of orientation soon after their cells are sealed.

(2) Materials within cells, possible odours and vibrations outside cells, or possible odours and glandular secretions in cell end walls influence larval orientation little, if at all.

(3) Larvae orientate correctly in extra long artificial cells (simulating natural ones and horizontally placed) in which they cannot touch both ends simultaneously.

(4) In natural cells or cells simulating natural ones, larvae defecate with their anterior ends touching the rough-textured end walls.

(5) Larval orientation is not influenced by cell ventilation.

(6) Worker and drone larvae do not orientate to gravity.

(7) Under artificial (and probably natural) conditions, the major factors controlling larval orientation are:—

(*a*) *Worker:* primarily texture of cell end walls (i.e. basal end smooth, capping end rough) and secondarily shape of cell end walls (i.e. basal end round, capping end flat).

(*b*) *Drone:* texture of cell end walls.

(*c*) *Queen:* gravity and possibly the rough texture (i.e. the cocoon of the lower end wall).

(8) Tactile sense organs at the extremities appear to be involved, and with queens, geotactic sense organs may also play some part. This needs further investigation.

THE ORIENTATION OF HONEYBEES TO THEIR HIVES. By J. B. FREE, *Rothamsted Experimental Station, Harpenden.*

Honeybees may stray into hives other than their own, particularly during their first flights or when their hives are moved to a new site. This 'drifting' behaviour, which is extensive when identical hives are arranged in regular formations, is undesirable because it may result in spread of disease, erroneous selection of queens and drones for breeding and lowering of average honey production.

When hives are in rows fewer worker bees drift from the end than from the centre hives resulting in the end hives gaining in bees. When hives are in repetitive patterns bees drift mostly to hives occupying similar positions in the pattern to their own. In some circumstances more bees drift in one direction than in the opposite direction. Although individual bees are more likely to drift from small to large colonies than *vice versa* the greater numbers flying from the large colonies may result in the small gaining numerically.

Drones drift two to three times as much as workers. More drones and workers from queenright colonies drift to queenless than to queenright colonies but drones expelled from queenright colonies do not drift to queenless ones. The amount queens drift is unknown.

Bees orientate to the colour in the immediate vicinity of their hive entrance and take little or no notice of the colour of the upper part of their hive. They learn a colour below their hive entrance better than one above. They do not learn combinations of colours. They distinguish between some symbols put immediately above the hive entrance. They learn the shape or size of their hive and its height above ground. They pay particular attention to the direction their hive faces. The distinctive odour of a colony does not appear to facilitate orientation of its bees directly.

Consequently beekeepers can reduce drifting by: arranging their hives irregularly, facing them in different directions, putting differently coloured boards immediately above or preferably below hive entrances, and having hive stands of different heights.

REFERENCES

Free, J. B. (1958). The drifting of honey-bees. *J. agric. Sci.*, **51**, 294-306.

Free, J. B. & Spencer-Booth, Yvette (1961). Further experiments on the drifting of honey-bees. *J. agric. Sci.*, (in press).

ENVIRONMENTAL FACTORS NECESSARY FOR THE MIGRATION OF LOCUST NYMPHS. By PEGGY E. ELLIS, *Anti-Locust Research Centre, London & Hope Dept. of Entomology, Oxford.*

Under natural conditions, large populations of locust nymphs live together in bands and spend a great deal of their time in wandering or marching. Nymphs of the Desert Locust, *Schistocerca gregaria* (Forsk.) have four main periods of marching. Provided dawn temperatures are above 15°C. there is an active period of marching at first light, triggered off by the increasing light intensity at dawn. Later, the nymphs bask in the sun. There is a second active period of marching during the late morning and another in the afternoon that appear to depend largely on changing temperatures. High temperatures at midday reduce or inhibit activity. If temperatures at sunset are above 28°C. then, after a short period of basking in the evening sun, the nymphs continue marching during the night until air temperatures have fallen to about 24°C. Laboratory experiments show that maximal marching can be obtained by many different combinations of factors. Some of the most important are changing temperatures, small air movements, a large number of hoppers in the band, and starvation for short periods. There are many examples of different factors interacting with one another; for instance, in the presence of food, air movements stimulate marching at higher temperatures, but have no effect or reduce marching at lower temperatures. Under conditions of starvation air movements also have no effect on marching activity.

A review of the relatively small amount of information available on the factors that influence the directions taken by bands, suggests that air movements are important. Young nymphs in particular tend to move down wind. Other factors, such as ground slope, areas devoid of vegetation and a tendency to keep moving in the same direction as the result of interactions with one another (gregarious inertia), may all interact with the orientating influence of the wind.

ORIENTATION AND DISPLACEMENT IN FLYING LOCUSTS. By ZENA WALOFF, *Anti-Locust Research Centre, Kensington, London.*

Freely flying locusts have an air-speed of 10-12 m.p.h., and factors affecting their orientation could thus be of importance in determining the direction of their migrations. There is no evidence that either photo-tactic or light-compass reactions are significant in this connection, for night flying solitary Desert Locusts appear to fly at random in relation to moon's azimuth, while locusts flying in swarms by day do not maintain any consistent orientation to the sun. Similarly, apart from behaviour on landing and on encountering strong head-winds, there is no evidence that flying locusts are orientated by wind perceived through changes in retinal velocity, for analyses of successive "double exposure" vertical photographs of locusts in full flight provided no indications that orientations altered in response to changes in angles of drift, in ground speeds, and in tracks, imposed by a fluctuating wind.

On the other hand, swarming locusts align on each other and fly in uniformly orientated groups which have been recorded photographically in formations with the mean spacing between fliers ranging from 1·5 to over 30 ft.; in the latter case the uniformity may have been imposed by a reaction to the swarm-mass. Such uniformity, however, does not extend throughout whole swarms, which typically consist of uniformly orientated groups moving in different and frequently changing directions; the continual cohesion of swarms is maintained by the turning back into the swarm of individuals or groups flying out beyond its perimeter. Simultaneous photographic recordings from the ground of orientations in passing swarms and determinations of their trajectories from the air have shown that the former were effectively random in relation to swarms' displacements, which were with the wind.

Downwind displacement during migration has now been found to occur in a variety of insects, and suggests the possibility that undirected flight on randomly changing orientations, unrelated to their ultimate destination, may represent the normal pattern of behaviour in a number of insect migrants.

THE MIGRATION OF DESERT LOCUST SWARMS: FACTS AND POSSIBLE IMPLICATIONS FOR BIRD MIGRATION.

By R. C. RAINEY, *Anti-Locust Research Centre, Kensington, London.*

Desert locusts make regular long-range migrations, over distances of thousands of kilometres, to a seasonal pattern which enables the species to exploit effectively the scanty and erratic rainfall characteristic of its typical habitats, where these migrations accordingly have a very important survival value.

It is, however, now clear that the part played by the orientation (heading) of the individual flying locusts, in determining the direction of these impressive migrations, is certainly very small and probably negligible. The considerable data now available on the directions both of large-scale seasonal migrations, and of the local movements of individual swarms, are in fact consistent with an effectively random orientation of the flying locusts. This inevitably results in a down-wind direction of displacement; and the seasonal pattern of locust migration, together with its biologically significant association with rainfall, necessarily emerges from down-wind displacement and the meteorological fact that convergent low-level wind-flow is essential for the production of signicant rainfall.

Migrating locusts thus appear very much as creatures of circumstance, with not only the directions but even the destinations of their spectacular flights largely if not wholly determined by the corresponding synoptic meteorology. This is in such complete contrast with the standard of navigation exhibited by birds that it has seemed, until recently, that the migrations of birds and of locusts must be two processes so fundamentally different that even the use of the same term was to be avoided.

The locust story may, however, suggest a possible mechanism by which birds might originally have begun to learn to migrate and to navigate, initially with sense-organs and central-nervous system of perhaps no more than reptilian standard. The first birds presumably may well have been poikilothermal, and perhaps accordingly mainly restricted to the tropics and subtropics, where the modern locust data show that even randomly-orientated flight, making possible the temporary colonization of the ephemeral habitats provided by the erratic rains of the semi-arid and arid zones, is of substantial survival value; the proverty of the fossil record of birds is consistent with the possibility of much of the evolution of the group having occurred under arid conditions. Might it perhaps have been the great planetary wind-fields, particularly the Trade-winds and the Inter-Tropical Convergence Zone (which are likely, on meteorological grounds, to have existed far back into geological time), which produced the first-seasonal displacements of initially randomly-orientated fliers, acting upon these primitively-equipped pioneer birds in a manner essentially similar to the way in which these wind-fields still appear to determine the migration of locusts? And was it perhaps population displacements, initially produced in this manner, which provided the 'familiarization flights' needed for the development of bird navigation to the impressive standard which it has now reached? The Inter-Tropical Convergence Zones show not only seasonal but also short-term fluctuations in position, which result in to-and-fro movements of locust swarms, thereby suggesting possibilities of elementary training of primitive birds in visual navigation by local familiarization flights repeated at intervals of days or weeks.

One might thus come to regard ability to navigate in flight as, geologically, a relatively recent refinement, rather than as a necessary first step in the evolution of bird migration. Even if the first birds were already capable of rudimentary terrestrial or marine navigation, as some modern reptiles may be, a mechanism comparable with that of locust migration might still have operated to give them sufficient opportunity to evolve solutions to the different and probably more difficult problems of aerial navigation.

APHID DISPERSAL AND ITS BEARING ON THE GENERAL CHARACTER OF INSECT MIGRATION BY FLIGHT.

By C. G. JOHNSON, *Rothamsted Experimental Station, Harpenden.*

The nature of the migration process in insects has been seen in terms of mass migration in butterflies, and as a flight, whose direction is controlled by the insects concerned. Passive drifters such as aphids were not regarded as true migrants; and dispersal and migration were seen as different processes.

But strong-flying locusts, apparently in control of their direction of displacement, are displaced along wind trajectories; this blurred the

distinction between migrants and passive drifters. Recent work with aphids showed that their aerial dispersal is best regarded as an evolved adaptation to scan the environment with a maximum of individuals. Thus the distinction between migration and dispersal is also blurred.

There are now a very large number of insect species especially in the aerial plankton which appear to be adapted to migrate and to disperse at the same time. The original breeding site, which is the locus of production for adult migrants, is relinquished and a transmigration taking various forms (from self-directed flight to passive displacement, from distances of a few yards to thousands of miles and involving different associated activities such as feeding and egg laying) ends with the selection of new hosts and habitats.

In view of the different types of flight involved in this process, it is difficult to characterize migration by one special kind of flight; but the ecological criterion of displacement from the breeding site and the acquisition of another is universal.

MIGRATION IN LEPIDOPTERA, COLEOPTERA AND DIPTERA WITH SPECIAL REFERENCE TO BEHAVIOUR. By C. B. WILLIAMS, *Rochester Terrace, Edinburgh.*

After a brief account of the known migration of two species of butterflies, and references to the migration of Hymenoptera Ladybirds and Syrphidae, certain aspects of behaviour shown by migrating insects were dealt with:

(1) The definiteness of flight migration as shown by their behaviour on reaching obstacles which when possible they avoid by rising over the top rather than by deviation.

(2) The simultaneous flight of many species in the same direction, and, of even greater interest, known cases when several species of insects (in one case two species of butterflies and the desert locust) have been observed flying in separate directions, the different species interlacing without interference with each other.

(3) The evidence for seasonal alteration or reversal of flight direction which is now known to occur in many species.

(4) The behaviour in relation to wind, giving examples where the flight has continued in a constant direction for days or weeks in spite of many changes in wind direction, and a few cases where changes of flight direction have occurred without any change of wind.

(5) Their relation of migration to population density showing that flight may be definite in direction but that individuals may be even a mile apart. In the case of the Monarch Butterfly aggregation of adults occurs before the southward autumn flight, and during it. This is followed by aggregated hibernation, but after the winter the bands break up, and the northern spring flight is almost always performed singly with aggregation.

ORIENTATED MOVEMENTS OF MARINE MOLLUSCS. By A. E. BRAFIELD, *Queen Mary College, University of London.*

Orientated movements are by no means uncommon among littoral molluscs. They may enable a mollusc to recover a site which affords protection from wave action and desiccation. Such movements have been described for a chiton (1) and for the small lamellibranch, *Lasaea rubra* (2). In both cases effective interplay between responses to light and gravity is involved.

The homing behaviour of limpets is extensively documented, but the method by which a limpet finds and recognizes its own scar is still obscure. Kristensen (unpublished) has recently shown that the mantle edge tentacles are not necessary for homing. He also confirmed that the outward track is not always retraced, and indicated that responses to light may play a part in homing.

Where the need for protection is less potent force, orientated movements may serve to aid a mollusc in maintaining its station on the shore. The bivalve *Macoma balthica*, for example, undertakes U-shaped feeding excursions over the sand flats at low water which are at first photopositive and later photonegative (3). Such movements have also been observed in other lamellibranchs, in the gastropod *Hydrobia ulvae* (R. Newell, in the press), and in winkles (4). Evans (in the press) has investigated a complex combination of phototactic and geotactic responses which serves to maintain populations of the Ghana winkle *Littorina punctata* in the zones in which they are most viable. Recent laboratory experimentation by Charles (5) has shown that winkles can orientate to plane polar-

ised light. The importance of such responses in the field is uncertain.

REFERENCES

(1) Evans, F. G. C. (1951). An analysis of the behaviour of *Lepidochitona cinereus* in response to certain physical features of the environment. *J. Anim. Ecol.*, **20**, 1.

(2) Morton, J. E. (1960). The responses and orientation of the bivalve *Lasaea rubra* Montagu. *J. mar. biol. Ass. U.K.*, **39**, 5.

(3) Brafield, A. E. & Newell, G. E. (1961). The behaviour of *Macoma balthica* (L.). *J. mar. biol., Ass. U.K.*, **41**, 81.

(4) Newell, G. E. (1958). The behaviour of *Littorina littorea* (L.) under natural conditions and its relation to position on the shore. *J. mar. biol. Ass. U.K.*, **37**, 229.

(5) Charles, G. H. (1961). The orientation of *Littorina* species to polarised light. *J. exp. Biol.*, **38**, 189.

ORIENTATION AND LEAPING BEHAVIOUR OF MIGRATING SALMONIDS AT FALLS AND OBSTRUCTIONS

By T. A. STUART, *Freshwater Fisheries Laboratory, Pitlochry.*

Laboratory and field observations and experiments have shown that the behaviour of migrating salmonids, adult and juvenile, when faced with a barrier or obstruction, can be correlated directly with the hydraulic conditions obtaining in the river channel.

It appears likely that the signal that stimulates the fish to move forward preparatory to the leap over an obstacle is related to the impact of falling water on the surface of a pool. As the force of the impact varied with changing discharge so also did the relative size of the fish that responded. The response also varied with the amount of air entrained in the water.

The stimulus to leap was found to be closely related to the presence of a standing wave (or hydraulic jump) and the location of the standing wave distant to the obstacle influenced the success of the leap. Thus in shallow fall pools and pools below sloping weirs the standing wave becomes located too far downstream for the fish to strike the crest of the fall on the upward arc of its trajectory. If the fish strikes the falling water on the downward arc it is immediately swept downstream. Optimum leaping conditions were obtained when the depth of the fall pool was increased so that the standing wave became submerged at the 'toe' of the fall, the ideal ratio of height of fall to depth of pool being 1:1·25.

All leaps in the laboratory and in the field were observed to be initiated at the surface of the pool (on the neutral point of the standing wave) and no fish was observed to approach in a run from a distance, laterally or vertically and perform a leap without a halt near the surface of the pool.

The great amplitude of the flexions of the fishes' body as it leaves the surface of the pool suggests powerful strokes of the tail near the surface as the main source of propulsion through the air. This action can be compared to the effort expended by the nest-building female whose powerful body flexions, by displacement currents, excavate the gravel in the river bed. In the latter case, in contrast to the disposition of the fins in the leaping fish, the pectorals and ventrals are rigidly distended and extended forwards thus acting as brakes to forward movement and directing the forces downwards and to the rear.

THE SEASONAL MOVEMENT OF TOADS (*Bufo bufo*).

By H. J. MOORE, *Clayesmore School, Blandford.*

The spring movement of toads to a lake in Dorset was described. The movement was found to be a radial congregation, rather than a linear migration, though more of the animals came from off the chalk lying higher to the East.

The movement spread over a period of from a fortnight to two months according to weather conditions.

The possible directive stimuli were discussed. It was not thought that the sound of calling males could carry far enough. They can be heard against a light breeze only up to 40 yards and were audible downwind up to 200 yards. Whatever the primary directive stimulus is, sound would play its part when the animals were close to the lake and probably be of importance in the final stages of congregation. Olfactory stimuli appear to offer the best hope but the sense of smell of *Bufo bufo* is not well deveoped as in the Natterjack (*B. calamita*). The difficulty of the odour of algal flora reaching toads against the wind was emphasized.

Visual memory by emigrating toadlets present certain difficulties and no emigration across the road of such young toads has been observed.

Finally the existence of a well-marked, but smaller-scale migration towards the lake in October and November was established. It had

been studied at Clayesmore and since reported from other areas. It is less efficient than the spring movement and differed in that the toads fed enroute, no pairing took place except on reaching water, the sex ratio was more even, and the orientation was less accurate, males tending especially to wander. Toads are physiologically in a condition to breed by the end of September and the accumulation of prolactin is thought likely to initiate their wandering. The movement was regarded as an abortive breeding cycle, that was interrupted by winter, and in particular by the low temperature of the water which was thought to be the explanation for no spawn having been found.

ORIENTATION IN DUCKS. By G. V. T. MATTHEWS, *The Wildfowl Trust, Slimbridge.*

Mallard caught at Slimbridge, Gloucestershire, and released at many points in various directions consistently fly off between North and West regardless of time of release, season of capture, sex, age, wind direction or topography of the release point. The direction is not maintained, subsequent recoveries being scattered at random. Orientation at release is stastically clear within 30 seconds and can therefore give a false impression of immediate position fixing when the home and "nonsense" directions coincide. The work on pigeons in Germany and North Carolina is open to criticism on this score.

The thickness of overcast needed to prevent sun-orientation is being assessed by photometry. At night the use of small 'sputnik' lights attached to the legs of the Mallard have fully confirmed star orientation and possibly moon orientation.

Mallard caught at Borough Fen, Northamptonshire, show a N.W. orientation in September, but later in the season no particular orientation is apparent. It is possible that this may be due to the influx of migrants with a different orientation. Birds caught at St. James's Park, London, fly predominantly between East and South. The part played by learning, possibly in relation to the topography of the 'home' area, is being investigated by rearing experiments.

Preliminary tests with Teal have indicated a S.W. 'nonsense' orientation in Britain, Holland and France.

THE NAVIGATION OF LAND-BIRDS: OVER THE SEA THE RADAR EVIDENCE. By D. LACK, *Edward Grey Institute of Field Ornithology, Oxford.*

Observations by high-power radar of migrants over the sea show that:

1. Migrants normally maintain steady tracks, both by day and by night.

2. They do not normally change direction with the change from daylight to dark or from dark to daylight, though presumably switching between solar and stellar navigation.

3. Their tracks are normally the resultant between a determined heading and the wind at the time, without allowance for lateral drift by a cross wind. However, migrants do not usually set out in a strong cross-wind.

4. Tracks were random for 6 per cent. of the periods analysed, the area of dis-orientation being local, and always associated with fog or rain. Visual observations show that low-flying migrants may maintain orientation in full overcast.

5. Migrants may head in at right angles on sighting the coast, and sometimes continue in a rather different direction over the land from that over the sea, or they may turn up-wind along a coast. More complex gradual changes in direction have sometimes been recorded by day in the southern North Sea. When land-birds are drifted far out over the Atlantic during the night, they may head back into the wind at daylight, in a direction nearly opposite to that in which they were previously flying.

6. Especially in autumn, migrants normally set out with a very light wind or a more-or-less following wind. Migration in a direction opposite to that normal for the season of year sometimes occurs with a head-wind.

MIGRATION AND ORIENTATION IN PINNIPEDIA AND CETACEA. By K. M. BACKHOUSE, *Charing Cross Hospital Medical School, Chandos Place, London, W.C.2.*

The Pinniedia are commonly considered to be migratory animals. *Callorhinus ursinus*, for instance, may travel thousands of miles throughout the North Pacific from its northern breeding grounds. This constitutes a wide feeding dispersal with little or no tendency for maintenance

of large migrating groups, but nevertheless the adult fur-seal returns to its own natal ground for breeding. Other land breeding seals, e.g. *Halichoerus grypus* have a much more localized dispersal. In the species some animals hardly leave the breeding area whilst others range more widely. *Phoca vitulina* probably disperses only so far from its breeding grounds as is necessary for food. Certain more polar forms, e.g. *Phoca groenlandica*, are bound to the ice for breeding and move with this during breeding, followed by a period at sea for feeding before returning north to the ice. In the majority of Pinnipedia, therefore, the migratory pattern, when present, tends to be one of a feeding dispersal varying in distance and according to species, rather than a formal migration and a collection upon the natal grounds for breeding.

No common movement pattern appears to exist therefore, even within seals of a single breeding colony on which migration orientation can be fixed.

Local orientation appears to be associated with use of sight, scent, hearing and by vibrissal sensation, but available evidence suggests that echo location is not used.

Some Cetacea feed in polar waters and migrate for breeding. *Eschrichtius glaucus* feeds close to the ice during the summer months. In the Autumn one stock calves in Korean waters, and the other in certain shallow bays of California. The Californian population follows a set course which differs for the northerly and southerly runs—a routine rigidly adhered to each year.

Some stocks of *Megaptera nodosa*, follow an accurate course north and south relative to New Zealand (Dawbin) but the species is not so localized in migration as *Eschrichtius*, there being a generalized north-south migration extending around the southern hemisphere. Other Cetacea, e.g. *Tursiops*, probably migrate relatively little except possibly at the limits of their range, movement being controlled largely by food movements.

Echo location is of tremendous importance for local orientation relative to obstructions, channels, in shallow water, food finding, etc., but there is no evidence to suggest that echo location can be of more than purely local value. As in the case of the Pinnipedia no common factor can be used to explain migration direction finding.

THE ACOUSTIC ORIENTATION OF BATS. By J. D. PYE (read by D. F. N. HARRISON), *Institute of Larngology and Otalogy, London.*

Acoustic orientation, or echo-location, by insectivorous bats is now well established and some idea of the speed and accuracy of the phenomenon has been obtained. Professor D. R. Griffin of Harvard University, has kindly lent a film, made with him by F. A. Webster and D. Cahlender, which clearly shows at greatly reduced speed the actions and cries of a bat as it captures mealworms tossed into the air. Nevertheless the mechanisms involved in this performance are not understood. Theories involving the measurement of echo-delay, by analogy with echo-locating machines, encounter severe physiological difficulties in explaining short range operation. Also it is shown that any system which hopes to account for the accuracy of the bat must utilise the full band-width of the bat's call.

A hypothetical mechanism is suggested which takes these facts into account and also helps to avoid the problems of masking, refractory period of the acoustic nerve and the central interpretation of echo information. Three modes are proposed, all involving the production of beat-notes between the call and its returning echo. The first two depend on the presence or absence of frequency modulation and the third on rapid movement of the pinnae. Their relative application is thus governed by the cries and behaviour of the bat, although Rhinolophids could probably use all three. This scheme provides possible explanations for the difference in performances between Vespertillionids and Rhinolophids and for some unusual features in the morphology and behaviour of species in both families. An electronic model allows all three modes to be tested with the human ear and is demonstrated by a short film.

OBSERVATIONS ON RANGE AND MOVEMENTS OF SHREWS. By JOY SHILLITO, *M.A.F.F. Infestation Control Laboratory, Guildford.*

The results of marking and recapturing a population of common shrews (*Sorex araneus*) in a small woodland in Exeter, from April 1958 to April 1960, have shown that their movements are closely related to their life history. In the summer, the juveniles are capable of consider-

able dispersal; this is of value when the population numbers are high and vegetational cover is good and it results in a more even distribution of the population. The subadults have small ranges over the winter time when food sources are deeper in the litter and growth and possibly activity are restricted. In spring, the shrews mature and the females increase their subadult ranges to larger breeding ranges which are well spaced in the wood. This is important for efficient utilization of food resources with a predatory animal. Finally the males move extensively; travelling freely between the widely spaced female ranges and leaving the wood. This movement enables them to find the females when they are in oestrus and allows for genetic interchange between populations. Incidental recaptures of *Sorex minutus* indicate that they have a similar organization but are generally more restricted in range.

The sudden occurrence and successive recaptures of fourteen water shrews from June to September 1959, showed that they were moving progressively through the wood. It has often been observed that this species of shrew is capable of prolonged excursions and their distribution is known to be irregular; it is suggested that *Neomys fodiens* may be a nomadic animal. When conditions in breeding areas become unfavourable they may disperse along hedgerows and through suitable country in small parties dispersing further as they go. These trapping results are thought to be a record of such a party which stayed from one to three months as the wood provided more food and space than the surrounding hedgerows.

PERCEPTION OF LINEAR MOTION. By E. G. WALSH, *Department of Physiology, University of Edinburgh.*

In the inner ear are found two linear accelerometers, the saccule and the utricle. An understanding of their behaviour would entail for each a knowledge of any relevant time constants and a three dimensional polar diagram showing the sensitivity to motion in different directions. Furthermore both the time constants and the polar diagrams might change with the orientation of the head because of the alteration in the gravitational biasing. Knowledge of any sort bearing on these problems is fragmentary and virtually non-existent for man and all other animals. Some information bearing on the properties of the system and its C.N.S. connections may be obtained by studying the perception of linear motion. Methods have been developed for producing whole body acceleration that are silent and free from vibration.

It was first necessary to establish the role of the vestibular apparatus. Observations on subjects totally submerged in water or paste showed thresholds within normal limits, similar observations were made on patients suffering from severance of the spinal cord. On the other hand deaf children with evidence of damage to the inner ear had great difficulty.

It has been established that the properties of the system do vary according to the orientation with respect to gravity. Following unilateral labyrinthectomy, the situation is simplified for analysis because of a reduction in the number of otolith organs from 4 to 2.

Other observations have been made with slow oscillations (1/3 to 1/9 c/s). There is a phase advance; the sensations lead the corresponding phase of the motion by 90°. On the other hand with more rapid movements (1 c/s) the sensations are in phase with the motion. It is suggested that there are signs here that the otolith apparatus responds satisfactorily to the frequencies encountered in normal locomotion but breaks down with slower oscillations—as may be produced by many forms of transport. A study of the time constants of the vestibular apparatus in different animals in relation to the types of motion to which the head is customarily subjected would be of interest.

MEDICAL ASPECTS OF MIGRATION IN MAN. By A. L. COCHRANE, *Sully Hospital, Penarth.*

As coalworkers' pneumoconiosis can only be diagnosed in life by means of a chest X-ray it is of considerable importance to relate the X-ray category of pneumoconiosis to pulmonary disability. For various reasons the only satisfactory method of investigating this is to examine the pulmonary function of random samples of defined mining communities stratified by age, sex, X-ray category and occupation. Such surveys have revealed interesting regional differences and of the hypothesis put forward to explain them the most probable seems to be the difference in

migratory loss suffered in the past by the regions surveyed.

To investigate this point further some evidence is presented about the differences between migrants and non migrants in one of the areas —the Rhondda Fach—in the last ten years.

FISH MIGRATION: PASSIVE DRIFT OR ORIENTATED MOVEMENT? By F. R. HARDEN JONES,
Fisheries Laboratory, Lowestoft, Suffolk.

Heape's definition of migration as "a class of movement which impels the migrants to return to the region from which they have migrated" is very apt for fish as the eggs, larval and juvenile stages are often carried hundreds of miles by water currents. To maintain themselves within an area the older fish must, at some time, migrate in the direction opposite to that of the current which dispersed the younger stages. Homing—the return to the parent nursery area—may be regarded as a biological mechanism for the exploitation of suitable environmental conditions in a particular region. There is no doubt that, of those salmon that do return to freshwater, the majority return to spawn in their Parent Stream: a critical review of the evidence suggests that the European eel returns to spawn in the Sargasso Sea—as Schmidt originally suggested. Herring, cod, and plaice all show some degree of homing, but the data at present available does not allow one to say how precise it may be. Little is known about the sensory mechanisms involved in the recognition of the Parent Spawning Ground or area. However, this can be called Pilotage, as the recognition of local "landmarks" is almost certainly involved.

It is not at all clear what level of homing is used in the long distance migrations that salmon, cod, herring, plaice, and probably the eel, make between their feeding and spawning areas. A simple contranatant theory of swimming against the current is not always convincing when one considers the currents involved, the cruising speed of the fish, and their reaction to a water current as studied under laboratory conditions. Sun navigation meets certain difficulties and, in the case of the Arctic cod, cannot provide a directional clue, as the sun is well below the horizon during the months that the fish move from Bear Island to the Norwegian Coast.

The simplest hypothesis that might account for the known facts would be one of passive drift in the ocean currents. On the continental shelves the tidal currents are more important. Many fish—cod, herring, plaice—carry out diurnal vertical movements from the bottom by day to midwater by night. Here migration may be achieved by passive drift at night—when the fish are off the bottom and have no fixed reference point for orientation, and they might be able to hold their position against the tide during the day when they are on or close to the bottom. Work being carried out at the Fisheries Laboratory, Lowestoft, goes some way to supporting this hypothesis, but a great deal remains to be known, particularly about oceanic and tidal currents, before one can decide whether or not such a relatively simple hypothesis can account for the facts of fish migration.

PROCEEDINGS OF THE SECTION OF ANIMAL BEHAVIOR AND SOCIOBIOLOGY (ECOLOGICAL SOCIETY OF AMERICA AND THE AMERICAN SOCIETY OF ZOOLOGISTS)

The following papers were read at the 1961 Annual Meeting held on the campus of Purdue University from August 28th to 31st. co-sponsored by the Section of Animal Behaviour and Sociobiology of the Ecological Society of America and of the American Society of Zoologists.

Abstracts of the papers are available in the *Amer. Zool.*, **1**, 1961.

Monday Morning, August 28th, 1961.
ANIMAL BEHAVIOR. I.
N. E. COLLIAS presiding.

MECHANISMS OF SOUND PRODUCTION IN THE MARINE CATFISHES, *Galeichthys* and *Bagre*. By W. N. TAVOLGA, *American Museum Natural History*.

SPECTOGRAPHIC ANALYSIS OF DOG SOUNDS. By J. P. SCOTT, *R. B. Jackson Memorial Laboratory*.

THE ACOUSTICAL LOCALIZATION OF PREY BY THE BARN OWL (*Tyto alba*). By R. S. PAYNE, *Cornell University*.

OLFACTORY DISCRIMINATION BY INDIVIDUALS OF *Peromyscus maniculatus* and *Peromyscus polionotus*. By ROBERT E. MOORE, *University of Texas*.

VARIATION IN BEHAVIOR AND TEMPERAMENT AMONG THREE RACES OF PEROMYSCUS. By L. R. DICE & P. J. CLARK, *University of Michigan and Cranbrook Institute of Science*.

INTERSPECIFIC SPATIAL RELATIONSHIPS AMONG SMALL MAMMALS. By K. R. BARBEHENN, *N.I.M.H.*

THE BEHAVIORAL RESPONSE OF FREE UINTA GROUND SQUIRRELS (*Cittellus armatus*) TO A TRAP. By D. F. BALPH, *Utah State University*.

BEHAVIORAL FACTORS ASSOCIATED WITH THE CESSATION OF GROWTH OF LABORATORY POPULATIONS OF PRAIRIE DEERMICE. By C. R. TERMAN, *Penrose Research Laboratory, Zoological Society Philadephia*.

THE EFFECT OF DENSITY AND AGGRESSION ON INTERACTION RATES IN WOODCHUCK POPULATIONS By F. H. BRONSON & D. E. DAVIS, *Pensylvania State University*.

Monday Afternoon, August 28th, 1961.
ANIMAL BEHAVIOR. II.
W. N. TAVOLGA presiding.

AN AMEBOID STAGE IN THE FEEDING BEHAVIOR OF THE HELIOFLAGELLATE PROTOZOAN, *Dimorpha floridanis*. By E. C. BOVEE & D. E. WILSON, *University of Florida*.

EFFECTS OF TIME AND INTERPOLATED PROBLEMS UPON RETENTION IN CHICKENS. By T. L. NASH, J. M. WARREN & M. W. SCHEIN, *Pensylvania State University*.

EARLY EXPERIENCE AND DISCRIMINATION LEARNING IN SWINE. By F. D. KLOPFER, *Washington State University*.

BEHAVIOR DURING A CONDITIONED REFLEX TRAINING PERIOD USED AS A MEASURE OF EARLY TRAUMA IN LAMB AND KID. By A. ULRIC MOORE & HELEN BLAUVELT, *Cornell University*.

FORM DISCRIMINATION IN THE SIAMESE FIGHTING FISH, *Betta splendens*. By J. C. BRADDOCK, ZORA I. BRADDOCK & RICHTER, H., *Michigan State University*.

Tuesday Morning, August 29th, 1961
ANIMAL BEHAVIOR. III.
J. C. BRADDOCK presiding.

INTERACTIONS AMONG CHICKENS IN DIFFERENT LEVELS OF THE SOCIAL HIERARCHY. By P. B. SIEGEL & H. L. MARKS, *Virginia Polytechnic Institute.*

INTER- AND INTRASPECIFIC DOMINANCE RELATIONSHIPS OF SYMPATRIC SPECIES OF INTERTIDAL HERMIT CRABS. By E. S. REESE, *University of Hawaii.*

COLOR PATTERNS AS INDICATORS OF MOTIVATION IN THE TELEOST FISH *Badis badis*. By G. W. BARLOW, *University of Illinois.*

SEXUAL BEHAVIOR OF THE COMMON GRACKLE, *Quiscalus quiscula*. By R. W. FICKEN, *Cornell University.*

SEXUAL RESPONSES OF ROOSTERS TO FULL AND PARTIAL MODELS. By B. T. CARBAUGH & M. W. SCHEIN, *Pennsylvania State University.*

THE EFFECTS OF VISUAL AND VOCAL STIMULI UPON THE REPRODUCTIVE ETHOLOGY AND PHYSIOLOGY OF PAIRED BUDGERIGARS (*Melopsittacus undulatus*). By B. F. BROCKWAY, *Cornell University.*

MOTOR COMPONENTS OF SEXUAL BEHAVIOR IN SHEEP. By E. N. BANKS, A. V. NALBANDOV & W. H. JOHNSON, *University of Illinois.*

THE RELATIONSHIP OF FAT DEPOSITION AND VERNAL MIGRATORY BEHAVIOR AS INDICATED BY ZUGUNRUHE IN *Zonotrichia leucophrys gambelii*. By J. R. KING & D. S. FARMER, *Washington State University.*

Tuesday Afternoon, August 29th, 1961.
ANIMAL BEHAVIOR. IV.
W. C. DILGER presiding.

THE SOCIAL BEHAVIOR OF GOATS DEPRIVED OF MATERNAL AND HERD CARE. By HELEN BLAUVELT, L. HERSHER & A. U. MOORE, *New York State College of Medicine.*

CLIFF EDGE RESPONSES OF GULL CHICKS. By J. T. EMLEN, *University if Wisconsin.*

CHANGES IN NEST-MATERIAL CARRYING BEHAVIOR OF F_1 HYBRIDS BETWEEN *Agapornis roseicollis* and *A. personata fischeri* DURING THREE YEARS. By W. C. DILGER, *Laboratory of Ornithology, Cornell University.*

NEST BUILDING AND REPRODUCTIVE BEHAVIOR IN *Agapornis* PARROTS. By R. B. KLOPMAN, *Cornell University.*

NEST-BUILDING AND BREEDING BEHAVIOR BY CASTRATED VILLAGE WEAVERBIRDS (*Textor cucullatus*). By N. E. COLLIAS, P. J. FRUMKES, D. S. BROOKS & R. J. BARFIELD, *University of California.*

THE USE OF A COMPUTOR IN A STUDY OF THE BEHAVIOR OF RATS DURING THE LITTER PERIOD. By ETHEL TOBACH, T. C. SCHNIERLA, R. LAUPHEIMER & K. CROSSMAN, *American Museum of Natural History.*

Wednesday Morning, August 30th, 1961.
A PROGRAMME OF BEHAVIORAL FILMS. PART I.
E. M. BANKS, Chairman.

PATTERNS OF DISPLAY IN IGUANID LIZARDS. By C. C. CARPENTER & KIRK T. MOSLEY, *University of Oklahoma.*

BREEDING BEHAVIOR OF THE BLACK-HEADED WEAVERBIRD (*Textor cucullatus*). By N. E. COLLIAS, *University of California.*

POPULATION DESTRUCTIVE INTRASPECIES FIGHTING. By H. BLAUVELT & U. MOORE, *New York State College of Medicine, Syracuse.*

COMPARATIVE STUDIES OF CANID BEHAVIOR. I. BIRTH AND MATERNAL BEHAVIOR. By B. E. GINSBURG, G. B. RABB & S. L. ANDREWS, *University of Chicago.*

COMPARATIVE STUDIES OF CANID BEHAVIOR. II. DEVELOPMENT OF SOCIAL BEHAVIOR IN RELATION TO EARLY EXPERIENCE. By B. E. GINSBURG, G. B. RABB & S. L. ANDREWS, *University of Chicago.*

TERRITORIAL BEHAVIOR IN UGANDA KOB. By HELMUT E. BUECHNER, *Washington State University.*

Wednesday Afternoon, August 30th, 1961.

A PROGRAMME OF BEHAVIORAL FILMS. PART II.

E. M. BANKS, Chairman.

SOCIAL INSECTS: THE HONEYBEE *Encylcopedia Brittanica Films* in collaboration with Dr. A. E. EMERSON.

THE ENCYCLOPOEDIA CINEMATOGRAPHICA, *Institut für den Wissenschaftlichen Film.*

PAARUNGSBIOLOGIE DER ANURAN, *Institut für den Wissenschaftlichen Film,* K. LORENZ & I. EIBL-EIBESFELDT

SEXUALVERHALTEN UND ERABLAGE BEIM ALPENMOLCH, *Institut für den Wissenschaftlichen Film,* K. LORENZ & I. EIBL-EIBESFELDT.

BABOON BEHAVIOR, I. DEVORE & S. L. WASHBURN, *University of California.*

PRESENTED BY TITLE

PATERNAL CARE OF THE YOUNG AND CONVULSIVE SEIZURES IN THE GRASSHOPPER MOUSE. By B. ELIZABETH HORNER, *Smith College.*

AQUATIC COURTSHIP OF THE WOOD TURTLE (*Clemmys insculptn*). By L. T. EVANS, *Jaffrey Center, New Hampshire.*

AN INTERPRETATION OF TURKEY COURTSHIP. By L. T. EVANS, *Jaffrey Center, New Hampshire.*

SOCIAL BEHAVIOUR OF RHESUS MONKEYS IN A TEMPLE HABITAT IN NORTHERN INDIA. By C. H. SOUTHWICK & M. A. BEG, *Ohio University, Athens.*

BOOK REVIEWS

Razvitiye psikhiki v protsesse evolyutsii organismov. (Development of mentality in the process of the evolution of organisms.) N. N. LADYGINA-KOTS. Sovietskaya Nauka, Moscow, 1958. 239 pp. including contents, bibliography, 75 text figures, no index.

In this abridged survey of a wide and complex field the author sketches development of organismic reactivity to the environment from protozoan sensitivity to fluctuations in light intensity through complex problem solving behaviour in the hominoid apes. Her introductory and concluding remarks state that the data advanced throughout the text support and amplify the philosophical positions of Engels, which are summarized in a quotation from his *Dialectics of Nature*: "From the first animals have arisen, mainly by means of the very greatest differentiation, the countless classes, orders, families, genera and species of animals, and, finally, those forms in which the nervous system reached its highest development—the vertebrates; and, again, finally, among these, that vertebrate in which nature arrived at a conception of herself, —man". With this set established, a series of chapters review the highlights of behavioural studies during the past 45 years on protozoa, coelenterata, annelids, arthropods, fish, amphibians, reptiles, birds, sub-primate mammals, and primates. One additional chapter deals with the communicative behaviour of apes and the reactions of animals (largely dogs and chimpanzees) to the human voice.

Each chapter starts with a brief description of the structural features, particularly those of the nervous system, distinguishing the group under consideration from the more primitive groups described in the preceding chapters. Emphasis is placed on the progressive complication of receptor systems and the relation of their development to the environment in which the animals live. Description of the structural and environmental correlates of behaviour is followed by examples of behavioural analysis drawn from the most outstanding studies available in Soviet and Western literature. Although ethological material (work of Tinbergen, Baerends, Lack, Von Frisch and others) is not neglected, classical conditioning experiments are emphasized. The facility with which a particular organism may be conditioned (in the Pavlovian tradition) is accepted as a yardstick of evolutionary progress. Instrumental conditioning and most current work with electrode implantation techniques are not discussed.

The last quarter of the book concerns observations on and experimental work with primates. This is the author's strong unit. In speculations on the genesis of *consciousness* (considered a uniquely human character) she attaches great importance to the development of the grasping, naked hand of apes. This evolutionary development is assumed to be intimately connected with the analysing and synthesizing processes characteristic of thinking. Moving through branches and gathering food with the hands stimulated development of the substrate of optic, tactile and kinesthetic receptors, plus the central integrating mechanism for these senses, which was necessary to the emergence of mental reactivity.

From the scope, brevity, and pitch of technical language it appears that the 2,500 copies of this edition will be of primary interest to Soviet intellectuals outside the zoological-behavioural professional community. In the West it will probably be of greatest interest to behavioural scientists interested in a broad brush treatment of the evolution of behaviour based on the author's familiarity with current Soviet work in this field. Two-thirds of the approximately 150 sources cited are Russian. Although, in itself, this will not serve as a source book on Soviet empirical results and methodology in this field, it is a handy, scholarly, and stimulating guide to original materials with which many Western workers are unfamiliar.

D.N.

The Kirtland's Warbler. BY HAROLD MAYFIELD. Cranbrook Institute of Science (1960). Pp. 242.

The life history of the Kirtland's warbler deserves the attention of all students of behaviour. This book describes the role of behaviour in the life of the individual and especially in the problem concerning the rarity of this species. The book is the product of joint research begun by Josselyn Van Tyne in 1930 and continued until his death in 1956. The author, Harold Mayfield, was a constant field companion of Dr. Van Tyne in the latter years and has brought the book to completion using both Van Tyne's and his own notes. The first part of the book contains several chapters describing the bird itself, its history, the ecology of the nesting

area, and the distribution and migration. The mating and territorial behaviour is the conventional warbler type. The male defends his territory by song and by fighting and mates with a female. The young are raised within the area. A curious aspect is that the birds tend to nest in colonies even though much suitable habitat is unpopulated. Other behaviour patterns are described in detail such as sleeping, eating, anting, and the vocalizations. The nesting information provides adequate data for the incubation period and behaviour of the adults during the nestling period and the fledging of the young. Although the population of Kirtland's Warblers consists of no more than 1,000 individuals, some 200 nests were observed during the 30-year study of this species. One feature of importance is that the incubation period is slightly longer (14 days) than that of most warblers. This feature undoubtedly assists the cowbird in its effective parasitism. Perhaps the most unique part of the book is a detailed analysis of the effect of the parasitism by cowbirds on the nest of the warbler. Although this part is not strictly behaviour the quality of the work deserves mention. In brief Mayfield concludes that the cowbird has recently entered the range of the Kirtland's Warbler and by very effective parasitism has substantially reduced the numbers of warblers. Indeed it may be largely responsible for the rarity of the species.

This book is a splendid example of the study of bird behaviour and bird habits in the field. Naturally there are no experimental aspects but the care in documentation fortifies the conclusions. With this contribution Mr. Mayfield can be classed among the outstanding amateur ornithologists in a group with Elliott Howard, Edgar Chance, and Margaret Nice. The book is beautifully printed and published by the Cranbrook Institute of Science and has a splendid frontispiece by Peterson showing a male, a female, and two fledgling warblers.

D.E.D.

BOOKS RECEIVED

The following books have been received and in appropriate cases will be reviewed as space permits in early issues.

Reshevsky, N.
Mathematical Biphysics. Vol. I.
Dover Publications Inc. $2.50

Rashevsky, N.
Mathematical Biophysics, Vol. 2.
Dover Publications Inc. $2.50

Lutz, F. E., Welch, P. L., Galtsoff, P. S. Needham, J. G.
Culture Methods for Invertebrate Animals
Dover Publications Inc. $2.75

Edited: Pool, W. A. (1960)
Veterinary Annual, 2nd issue.
John Wright & Sons Limited. 42s.

S.E.B. Symposium Number 14
Models and Analogues in Biology
Cambridge University Press 50s.

Lockley, R. M. (1961)
The Pan Book of Cage Birds
Pan Books Limited 2s. 6d.

Buytendijk, F. J. J.
Pain
Hutchinson & Company (Publishers) Ltd. 25s.

Editor: Farnsworth, P. R. (1961)
Annual Review of Psychology, Vol. 12
Annual Reviews, Inc. $7

Voous, K. H. (1960)
Atlas of European Birds
Nelson 70s.

Edited by Birney, R. C. & Teevan, R. C.
Instinct
D. Van Nostrand Company Inc. 11s. 6d.

Edited by Birney, R. C. & Teevan, R. C.
Reinforcement
D. Van Nostrand Company Inc. 11s. 6d.

Monnier, M. & Gangloff, H.
Atlas for Stereotaxic Brain Research on the Conscious Rabbit
D. Van Nostrand Company Limited 63s.

ERRATUM

The Editor regrets that the authors of the paper "The Toxic and Behavioural Effects of Reserpine on Cats", summarised on page 111 of Vol. IX, 1 & 2, were incorrectly printed as W. A. Beresford, J. C. Cole and P. Glees. He understands that the authorship should have been given as W. A. Beresford and P. Glees.

The Structural Basis of Behaviour

J. A. DEUTSCH

An original and provocative treatment of topics of fundamental importance to psychology and the study of animal behaviour. Dr Deutsch presents a set of theories to explain various kinds of behaviour, in terms of mechanisms that might be found in animal nervous systems or built as machines, and describes experiments which support these theories. 30*s. net*

Current Problems in Animal Behaviour

EDITED BY W. H. THORPE & O. L. ZANGWILL

A collection of essays by a group of Cambridge scientists bridging the gap between the work of the comparative zoologist and the experimental biologist on various problems in the behaviour of animals, including man. Each contributor considers work significant to the study of behaviour in general. 45*s. net*

CAMBRIDGE UNIVERSITY PRESS

ANIMAL BEHAVIOUR

J. L CLOUDSLEY-THOMPSON

". . . cannot be praised too highly. The author brings together a great deal of zoological fact which is as interesting as it is unobvious."

The Guardian

". . . highly recommended to the biologist with an interest in animal behavour."

Animal Breeding Abstracts

16 *half-tone plates, numerous line drawings*

Price 15s. net

OLIVER & BOYD

Tweeddale Court, 14 High Street
Edinburgh 1

ANIMAL BREEDING ABSTRACTS

The journal of the Commonwealth Bureau of Animal Breeding and Genetics

It covers the world's published research on breeds, breeding, productivity, growth, genetics and reproduction of all farm livestock, poultry, fur bearers and other animals of economic importance, as well as the small laboratory mammals.

Each issue contains a review article on some aspect of current research.

Published quarterly at the beginning of March, June, September and December, at 90/- per annum.

Subscriptions and enquiries to
Commonwealth Agricultural Bureaux
Central Sales, Farnham Royal
Bucks., England

Baillière, *Tindall & Cox*

offer an expert service for Books and Periodicals

Any book published in Great Britain can be obtained from the Sales Department of Baillière, Tindall and Cox, usually by return of post. Our agencies in the United States enable us to supply any American book, and all Continental books can be supplied very quickly. Subscriptions are accepted for all British, American and Continental Periodicals. When in London, visit our bookshop.

We compile lists of all reference works, books and monographs on any subject, giving authors, titles, date, pages, price, etc. We send announcements of new and forthcoming books and we keep you up to date on any subject in which you are interested. Detailed prospectus and catalogues of books of major importance are circularized regularly. All information is free of charge and without obligation.

7 & 8 Henrietta Street, London, WC2

A GLOSSARY OF SOME TERMS

USED IN THE

OBJECTIVE SCIENCE OF BEHAVIOR

By William S. Verplanck

Provides an empirical vocabulary in the science of human and animal behaviour.

Familiarizes readers with developments in the study of animal behaviour.

Clarifies concepts used by behaviourists and ethologists.

Second Printing **PRICE $1.00**

American Psychological Association

1333 SIXTEENTH STREET, N.W., WASHINGTON 6, D.C., U.S.A.

DICTIONARY OF BEEKEEPING TERMS

WITH ALLIED SCIENTIFIC TERMS
edited by Dr. Eva Crane

now available in two volumes

VOLUME I:
ENGLISH — FRENCH — GERMAN — DUTCH

VOLUME II:
ENGLISH — ITALIAN — SPANISH

each volume is available bound in cloth at 16/- ($2.80), or bound in board at 12/6 ($2.25).

The two volumes together make it possible to translate the 1500 terms listed from any one of the six languages represented into the other five. About half the entries are zoological terms.

BEE RESEARCH ASSOCIATION

Hon. Publications Secretary, 11 Poplar Grove, Maidstone, Kent

THE BRITISH TRUST FOR ORNITHOLOGY

is a unique organisation devoted to the encouragement and promotion of
RESEARCH
into the
LIVES, HABITS AND NUMBERS
of
BRITISH BIRDS

Quarterly Journal, *Bird Study* (edited by Dr. J. C Coulson) free to members: publishes *Bird Migration* (editor Kenneth Williamson) bi-annually, 3s. 6d. each post free; organizes Bird Ringing Scheme, Nest Record Scheme, Census of Heronries; sponsors investigations organized by members; jointly administers Alexander (Reference) Library; Lending Library service; Grants to aid research; Meetings all over the country; 80 Regional Representatives in the British Isles.

Full details of membership from
THE SECRETARY, B.T.O.
2 KING EDWARD STREET, OXFORD

VALUABLE RESULTS OF BEHAVIOUR RESEARCH

ZEITSCHRIFT FÜR TIERPSYCHOLOGIE

JOURNAL OF ANIMAL PSYCHOLOGY

EDITED IN COLLABORATION WITH LEADING EXPERTS

by

PROF. DR. O. KOEHLER and **PROF. DR. K. LORENZ**

Freiburg/Br. Seewiesen/Obb.

Zeitschrift für Tierpsychologie publishes original works and lectures about the whole field of research of behaviour and animal psychology in German, English, French and Italian. Each essay is followed by a short summary in German and English.

Articles included in vol. 18 (1961), Issues 1 and 2.

SCHNEIRLA, T. C. The Behavior and Biology of Certain Nearctic Doryline Ants Sexual Broods and Colony Division in *Neivamyrmex nigrescens.*

EIBL-EIBESFELDT, I. Eine Symbiose zwischen Fischen (*Siphamia versicolor*) und Seeigeln.

LORENZ, K. Phylogenetische Anpassung und adpative Modifikation des Verhaltens.

FROMME, H. G. Untersuchungen über das Orientierungsvermögen nächtlich ziehender Kleinvögel (*Erithacus rubecula, Sylvia communis*).

Please ask for our special prospectus !

VERLAG PAUL PAREY IN BERLIN AND HAMBURG

Berlin SW 61, Lindenstrasse 44/47, Germany

ANIMAL PRODUCTION

JOURNAL OF THE BRITISH SOCIETY OF ANIMAL PRODUCTION

Contents of Volume 3, Part 3, October, 1961

ALBA, J., CORTA, E. V. & ULLOA, G. Influence of natural service on length of oestrus in the cow.
ARMSTRONG, R. W. & CAMERON, A. E. Hexoestrol implantation of Blackface wether lambs.
BELLIS, D. B. Requirements of bacon and heavy pigs for certain essential amino acids.
BRUMBY, P. J. Relationship of genetic merit to herd differences in milk production.
DICKINSON, A. G. Modification of gestation length in cattle by environment.
DODSWORTH, T. L. & BALL, C. Treatment of beef cattle with tranquillisers and antibiotics.
DUCKWORTH, J. E., COOPER, M. McG., DUNKIN, A. G., TAYLOR, J. M. & HOLMES, W. Progeny testing of bacon pigs at Wye College.
HOLMES, W., JONES, J. G. W. & DRAKE-BRACKMAN, R. M. Feed intake of grazing cattle. II. The influence of size of animal.
KERR, J. A. M., BROWN, W. O. & MORRISON, J. Nutritive value of silage self-fed to fattening cattle.
LODGE, G. A., McDONALD, I. & MACPHERSON, R. M. Relative influence of birth-weight and creep-feed consumption on weights of sucking pigs.
LODGE, G. A., McDONALD, I. & MACPHERSON, R. M. Weight changes in sows during pregnancy and lactation.
PRESTON, T. R., GREENHALGH, I., BOYNE, A. W., CRICHTON, J. A., ROLFE, E. J., BROWN, A. & DODSWORTH, T. L. The effect of hexoestrol on eating quality of beef and lamb.
RENDEL, Jan, & GAHNE, Bo. Parentage tests in cattle using erythrocyte and serum transferrins.
WALKER, E. A. & TAYLOR, J. H. Effect of parenterally administered iron upon the growth of piglets.

ANNUAL SUBSCRIPTION **45s.** **(U.S.A. and CANADA $7.50)**
SINGLE PART **17s. 6d.** **(U.S.A. and CANADA $2.75)**

OLIVER AND BOYD LTD.

Tweeddale Court, 14 High Street, Edinburgh, 1

end